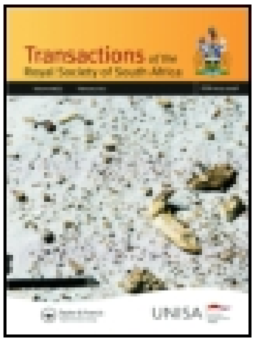

Transactions of the Royal Society of South Africa

ISSN: (Print) (Online) Journal homepage: https://www.tandfonline.com/loi/ttrs20

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To cite this article: Patricia M. Holmes , Karen J. Esler , Brian W. van Wilgen & David M. Richardson (2020): Ecological restoration of ecosystems degraded by invasive alien plants in South African Fynbos: Is spontaneous succession a viable strategy?, Transactions of the Royal Society of South Africa, DOI: 10.1080/0035919X.2020.1781291

To link to this article: https://doi.org/10.1080/0035919X.2020.1781291

Published online: 15 Jul 2020.

Transactions of the Royal Society of South Africa, 2020
https://doi.org/10.1080/0035919X.2020.1781291

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Ecological restoration of ecosystems degraded by invasive alien plants in South African Fynbos: Is spontaneous succession a viable strategy?

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Ecological restoration is a global imperative to reverse widespread habitat loss and degradation, including by invasive alien plants. In South Africa's Core Cape Subregion, alien tree invasions are widespread and their control continues to be a major undertaking. As funding is limited, active restoration interventions are rarely implemented and the focus is on invader removal – the assumption being that ecosystems will self-repair. This paper reviews research findings from the past three decades to assess in which situations spontaneous succession is a viable strategy for restoring alien-invaded ecosystems. We found that ecosystems can self-repair, provided that key biotic and/or abiotic thresholds have not yet been crossed. Self-repair has been observed in many cases where dense invader stands with short residence times have been cleared and where diverse native plant growth forms survive, either in the above-ground vegetation or in soil seed banks. However, several factors influence this generalisation, including the identity of the invader, the ecosystem type, and the efficacy of alien control. Thresholds are crossed sooner with invasions of alien *Acacia* and *Eucalyptus* species than those of *Hakea* and *Pinus* species, resulting in lower potential for spontaneous recovery. Lowland fynbos ecosystems are less resilient to invasion, and have a lower capacity for self-repair, than mountain fynbos ecosystems. Poorly implemented alien plant control measures can result in a resurgence of the invader to the detriment of native species recovery. We outline some management principles for optimising spontaneous succession potential and integrating alien control and restoration interventions.

Keywords: **active restoration; biological invasions; Mediterranean-type ecosystem; passive restoration; restoration ecology**

INTRODUCTION

Over the past few decades, ecological restoration has emerged as an essential intervention to counter the intensifying negative impacts that growing human societies exert on natural environments and on the planet as a whole (Gann *et al.*, 2019). These negative impacts are particularly acute in global biodiversity hotspots, such as the Core Cape Subregion (CCS) of South Africa, where conversion of natural vegetation for agriculture and urban development may result in the extirpation of local ecosystems and associated endemic species (Rebelo *et al.*, 2011).

Estimates of the extent of land modification and degradation amount to 66% of global land surface and the annual economic costs arising from these impacts are in the order of 10–17% of global gross domestic product (GDP) (Crossman *et al.*, 2017). For the CCS, the most recent estimate is 31% land conversion by 2014, excluding land degradation by overgrazing or dense alien invasion. Habitat loss is concentrated in the lowlands from expansive agriculture and human settlements and many lowland ecosystems are highly threatened (Skowno *et al.*, 2019). The direct and indirect use values of CCS natural ecosystems were estimated as exceeding 10% of regional gross geographic product (Turpie *et al.*, 2003), indicating that loss of habitat and degradation may represent a considerable economic loss to the region. In response to such global environmental challenges, the United Nations (UN) declared 2021–2030 the "decade on ecosystem restoration" (https://www.decadeonrestoration.org/). The UN declaration aims to massively scale up the restoration of degraded lands as a proven mitigation measure against global warming and to improve the flow of ecosystem goods and services (such as water supply and food security) that are essential for human wellbeing. It is generally acknowledged that to hold global temperature increases to between 1.5 and 2 °C, restoration of degraded ecosystems would be essential (Morecroft *et al.*, 2019). In order that global society secures a net gain in the extent and functioning of native ecosystems, conservation management efforts that seek to halt degradation in natural ecosystems need to be augmented by restoration of degraded lands (Gann *et al.*, 2019). Many countries including South Africa are signatories to international treaties advocating ecological restoration, such as the Bonn

Published online 15 Jul 2020

Challenge (www.bonnchallenge.org), Sustainable Development Goal 15 of the United Nations (https://unstats.un.org/sdgs/report/2016/goal-15/) and the Convention on Biological Diversity Aichi Targets (https://www.cbd.int/sp/targets/). Locally, South Africa's National Biodiversity Framework (Government Gazette No. 32474, 2009) summarises the actions required to conserve and restore South Africa's natural ecosystems.

This paper reviews research findings from the past three decades to assess in which situations spontaneous succession is a viable strategy for restoring alien-invaded ecosystems. All authors are intimately familiar with restoration in the CCS and have each spent >30 years in research and management in the region. Our review is thus based on personal knowledge of the literature, and has been substantially reinforced by the production of a recent comprehensive review of the field of biological invasions in South Africa (van Wilgen *et al.*, 2020).

Ecosystem degradation, alien plant invasion and restoration

The spread of alien (non-native) plant species, like climate change, is a significant but insidious global threat to natural ecosystems that has resulted from trade networks and deliberate or accidental species introductions (Wilson *et al.*, 2009, 2014). Invasion success depends on characteristics of the introduced species, such as those linked to propagule pressure, as well as those of the invaded community, including abiotic and biotic conditions and species interactions (Richardson & Pyšek, 2006; Catford *et al.*, 2009; Le Roux *et al.*, 2020). Those alien species that naturalise or escape from cultivation can become invasive and spread across the landscape to eventually dominate and suppress native species (Richardson *et al.*, 2000). In the worst cases, such invasions can dramatically change ecosystem characteristics, such as vegetation structure, dynamics and functioning, to the detriment of biodiversity and the flow of ecosystems goods and services (Gaertner *et al.*, 2014). An example of where invasion of alien plants has driven a regime shift that is difficult or impossible to reverse is in the Great Basin of North America, where the introduced European annual cheatgrass (*Bromus tectorum*) spread with livestock grazing to dominate vast areas, replacing native steppe vegetation (Mack, 1981). Cheatgrass, a highly flammable winter annual grass, has promoted the occurrence of summer fires, drastically increasing the frequency of fires, thereby destroying or damaging native shrubs and grasses (D'Antonio & Vitousek, 1992). Through this changed fire regime, cheatgrass creates a reinforcing feedback loop to its own benefit, resulting in negative impacts to rangeland productivity and biodiversity.

The Society for Ecological Restoration (SER) defines ecological restoration as "the process of assisting the recovery of an ecosystem that has been degraded, damaged or destroyed" (Gann *et al.*, 2019; Box 1). The discipline of restoration ecology seeks to provide knowledge to facilitate the effective application of ecological restoration. Ecological restoration aims to move a degraded ecosystem along a trajectory of recovery towards a reference ecosystem, while allowing for local and global changes. The "restorative continuum" concept is broader and incorporates other forms of environmental repair (Gann *et al.*, 2019) and it is thus a useful construct for setting appropriate goals and related restorative actions across a spectrum of degradation. At the most severe extreme of the continuum, for example following surface mining, restoring to a historical reference ecosystem may be impossible or impractical due to the extreme nature of biotic or abiotic modifications. At the other extreme are degraded ecosystems with potential for full recovery, either through spontaneous succession following removal of the degrading factor (passive restoration) or including manipulation of biotic and/or abiotic conditions (active restoration).

Box 1. Glossary of Terms

Active restoration – the management approach that requires further interventions aimed at assisting the recovery of the degraded ecosystem after the degrading disturbance is removed or reduced (e.g. the re-introduction of extirpated native species)
Core Cape Subregion (CCS) – distinctive floral region situated at the southwestern tip of Africa between 31° and 34° 30′ S, formerly called the Cape Floristic Region (CFR), and now considered a subregion of a larger area called the Greater Cape Floristic Region
Ecological restoration – the process of assisting the recovery of an ecosystem that has been degraded, damaged or destroyed
Ecosystem resilience – the degree, manner and rate of recovery of ecosystem properties after a disturbance
Ecosystem thresholds – points beyond which a change in biotic or abiotic conditions will move an ecosystem to a different ecological state
Follow-up control – repeated control of regrowth and recruitment of the target alien species after an initial control treatment
Integrated control – implementation of different complementary control methods to achieve a more sustainable level of control (e.g. using fire, mechanical, chemical and/or biological control methods in appropriate combinations)
Landscape context – the influence of the broader area in which an ecosystem is embedded that may influence the natural disturbance regime, the flows of resources and biotic interactions
Passive restoration – the management approach that relies on spontaneous succession after the degrading disturbance is removed or reduced
Reference ecosystem – an extant, intact site that displays the expected biophysical and vegetation structure, function and composition characteristics and can serve as a reference model for a degraded ecosystem
Rehabilitation – management actions that aim to reinstate a level of ecosystem functioning on degraded sites, where the goal is renewed and ongoing provision of ecosystem services rather than the biodiversity and integrity of a designated native reference ecosystem
Remediation – a management activity, such as the removal or detoxification of contaminants from soil and water, that aims to remove sources of degradation
Restoration ecology – the scientific study of repairing and managing degraded ecosystems through human intervention
Restoration potential – the potential of a degraded ecosystem to spontaneously recover after removal or reduction of the degrading factor
Restorative continuum – a spectrum of activities (including remediation, rehabilitation and ecological restoration) that directly or indirectly support or attain at least some repair of ecosystem attributes that have been lost or degraded
Self-repair – ability of an ecosystem to recover spontaneously following a perturbation
Spontaneous recovery – natural regeneration that leads to recovery of ecosystem structure and function after a disturbance
Spontaneous succession – natural regenerative processes following a disturbance

Restoration outcomes are highly variable and are potentially influenced as much by landscape characteristics, such as degree of habitat fragmentation, as local factors (Leite *et al.*, 2013). A review by Suding (2011) found that where native species and abiotic processes persisted, spontaneous succession occurred, whereas incomplete recovery was attributed to local and landscape constraints, including shifts in species distributions and legacies of past land use. In some restoration attempts little or no recovery occurred, owing to factors such as strong species' feedbacks or shifts in regional species pools. Reviews of invasive plant control experiments and management examples indicate that revegetation success was not always assessed, but when addressed was frequently complicated by re-invasion of the target invader or secondary invasions of other alien species (Reid *et al.*, 2009; Kettenring & Adams, 2011; Pearson *et al.*, 2016). These authors make a strong case to pre-empt re-invasion through anticipating the need for less damaging invader control methods and/or active restoration of native species.

The extent to which spontaneous succession is enough to restore degraded land depends on several factors, besides the landscape context and intensity or extent of degradation. Thus, an ecosystem's natural disturbance regime, recruitment dynamics and abiotic environment are likely to mediate the potential for spontaneous succession. For example in tropical forest ecosystems, where seed dispersal by animals and shrub or tree cover are usually important facilitators of colonisation by target tree species, Crouzeilles *et al.* (2016) found that spontaneous succession success depended on the landscape context, disturbance type, and the time elapsed since restoration interventions began. Prach and Moral (2015) noted that passive and active approaches have advantages and disadvantages depending on the ecosystem type and context (Box 2). Furthermore, active restoration may not always be faster than passive restoration, and there may be situations in which it is preferable to allow sufficient time for spontaneous succession to occur, as in European old fields (Dölle *et al.*, 2008). Most of the recent literature comparing the outcomes of passive and active restoration approaches worldwide deals with tropical forest and riparian ecosystems (Box 2).

Box 2. Passive versus active restoration approaches – summary of global comparisons

Global reviews and studies comparing passive and active approaches deal mainly with tropical forests and riparian ecosystems. Several studies report on restoration of degraded prairies, grasslands and meadows and a few address Mediterranean-type ecosystems such as fynbos and coastal sagebrush. This bias is probably largely attributable to the fact that most ecological restoration research is done in these ecosystems generally.

In tropical forest ecosystems variable results are reported (Brancalion *et al*., 2016; Trujillo-Miranda *et al*., 2018) with a dichotomy of opinion favouring passive versus active restoration approaches that relate mainly to the landscape context and type of degradation (Meli *et al*., 2017). Passive approaches may be fraught with arrested succession (Bechara *et al*., 2016) or slow to work where more extensive areas are dominated by grasses that prevent tree recruitment through competition or fire (Kamo *et al*., 2002). Caughlin *et al*. (2016) noted that rates of secondary succession vary widely depending partly on landscape features that are difficult to replicate. For example, their models indicated that seed rain is important for secondary succession where patches are near a threshold for arrested succession, but less important when seed availability is not limiting at the landscape scale. In the former scenario, active restoration by applied nucleation or plantation methods of tree introductions are recommended (Corbin & Holl, 2012; Gerber *et al*., 2017). Enrichment planting of key characteristic forest species is recommended for both passively and actively restored sites (Trujillo-Miranda *et al*., 2018). In contrast to old field areas, logged sites frequently restore well passively (Crouzeilles *et al*., 2016). It has been noted that the benefits of active forest restoration may be outweighed by costs (Birch *et al*., 2010). Innovative approaches, such as combining short-term commercial *Eucalyptus* plantation rows with forest restoration plantings, could partially offset the costs of active ecological restoration (Brancalion *et al*., 2019).

Passive restoration approaches generally work well in headwater and transitional riparian ecosystems, so long as the surrounding catchment contains relatively intact vegetation and has no major impoundments (Kauffman *et al*., 1997; Blanchard & Holmes, 2008; Dobkin et al., 1998; Hough-Snee et al., 2013; Batchelor *et al*., 2015; Muller *et al*., 2016). In riparian ecosystems, native propagules may persist in the soil seed bank (Vosse *et al*., 2008) or else are water-dispersed from upstream remnants, providing good potential for passive restoration (Galatowitsch & Richardson, 2005). Exceptions where active restoration is recommended include reaches that are highly degraded by alien woody plant invasions, such as *Tamarix* spp. in the USA (Taylor & McDaniel, 2004) and *Eucalyptus camaldulensis* in South Africa (Ruwanza *et al*., 2013c). Dense invasions of *Acacia* species in riparian ecosystems may also require active restoration in some situations (Reinecke *et al*., 2008). Gornish *et al*. (2017) recommend assessing the context for riparian restoration before selecting a technique: passive restoration may be quite rapid, and more useful where dominance of a pioneer species could arrest the threat of erosion, whereas in other situations active restoration to increase native cover and diversity may be more appropriate. In the case of *Eucalyptus* invasion in riparian ecosystems where Afrotemperate forest is the restoration goal, a phased approach has been recommended, whereby alien trees are cut in strips rather than clear-felled to prevent soil and bank destabilisation while providing space to interplant native trees or allow recruited native trees to grow (Geldenhuys *et al*., 2017; Hirsch et al., 2020).

European old fields (Dölle *et al*., 2008; Ruprecht, 2006) and even quarries (Řehounková & Prach, 2008) restored well by spontaneous succession given sufficient time, indicating that propagule sources of local species in these ecosystems are adequate to launch colonisation of highly-disturbed sites over moderate distances. Over a few decades, vegetation succession developed towards the local climax ecosystem, e.g. woodland, meadow or wetland, depending on local biophysical conditions (Dölle *et al*., 2008).

Research from the highly threatened and transformed North America prairie suggests that ecological restoration of old fields is very slow, whether involving active or passive methods (Kindscher & Tieszen, 1998). A combination of passive and active approaches is usually needed to optimise restoration along a trajectory to recovery; methods typically involve the use of one or more of the following: prescribed burning, grazing, soil fertility amendment, and the active planting or sowing of native species. For example, (Blumenthal *et al*., 2003) found that carbon addition improved native plant establishment and weed suppression. Middleton *et al*. (2010) found that planting seedlings and sowing seeds gave the best biodiversity outcome.

In most studies from Mediterranean-type ecosystems, active restoration is recommended for old fields or areas highly degraded by invasive species. In Chile, where recurrent burning in degraded shrubland and woodland is the major threat to restoration efforts, Cerdà *et al*. (2009) recommended native plant re-introduction and control of alien bamboo to improve outcomes. In coastal sage scrub DeSimone (2011) recommended native species re-introduction following control of artichoke thistle. Rayburn *et al*. (2016) found that degraded grassland in California lacked a native seed bank and that active restoration was needed. Gentili *et al.* (2015) made a similar recommendation for degraded grasslands in Italy. In a review of South African renosterveld old-field restoration studies, Ruwanza (2017) found that factors inhibiting ecological restoration interact to lock the system in a degraded state; they recommend an integrated approach using multiple methods to improve restoration outcomes.

Alien plant invasion in South Africa's Core Cape Subregion

Invasion of alien plants is a major threat to biodiversity and ecosystem services across most biomes of South Africa. Last century, scientists in the CCS recognised the linkage between alien tree invasions and reduced water yields from mountain catchments and rivers (Prinsloo & Scott, 1999; van Wilgen *et al.*, 2016a). In this water-limited country, they convinced government to invest in invasive alien plant control through a dedicated programme. Thus in 1995 the "Working for Water" (WfW) expanded public works programme was initiated in the CCS, then was expanded countrywide. WfW prioritised job creation and skills training by using invasive alien plant clearance in riparian zones and water catchments as the employment vehicle. It was generally assumed that native vegetation would restore itself through spontaneous succession following control of the invasive aliens (van Wilgen & Wannenburgh, 2016).

Although alien trees are the main focus of this review, herbaceous alien species also pose significant challenges to conservation and restoration in more degraded CCS habitats, particularly in the lowlands, as do alien aquatic plants in the waterways (Musil *et al.*, 2005; Cilliers *et al.*, 2009). In mountain fynbos ecosystems, alien pines (especially *Pinus pinaster* and *P. radiata*) and hakeas (especially *Hakea sericea* and *H. gibbosa*) are the most widespread and troublesome invaders (Wilson *et al.*, 2014). These species are pre-adapted to the nutrient-poor soils, the Mediterranean-type climate and fire regime. Their seeds are stored in fireproof structures in the canopy, are released after fire kills the plant, and are dispersed over great distances by wind. Like many fynbos species, these serotinous aliens are obligate reseeders; they rely on seed regeneration after fire. In theory, they should be straightforward to control as no herbicide is required; if they are felled before maturity, or a year or two before a prescribed fire, seed release and/or survival in the environment should be low (van Wilgen *et al.*, 1992). Yet, despite some early success (Esler *et al.*, 2010) during the past three decades these species have continued spreading and forming dense stands over large areas, outstripping the ability of WfW contract teams to control them (van Wilgen *et al.*, 2016b). Several introduced biological control agents have established on *Hakea sericea* and have reduced the reproductive output of the species (Moran & Hoffmann, 2012). Subsequently, over 15 years, *H. sericea* had a low relative increase in occurrence compared to pines, which do not have biological control (Henderson & Wilson, 2017).

In lowland fynbos ecosystems, acacia species (especially *Acacia saligna* and *A. cyclops*) and myrtle (*Leptospermum laevigatum*) are the most problematic alien tree invaders, although pines and hakeas have invaded some areas (Wilson *et al.*, 2014). Acacias are difficult to clear because they accumulate large banks of long-lived seeds in the soil, and some species (notably *A. saligna*) resprout vigorously after fires or if not cut sufficiently close to the soil surface (Strydom *et al.*, 2019). They also grow more quickly than pines and hakeas because of their capacity to fix nitrogen, and may rapidly outcompete fynbos species and exert a legacy of soil-enrichment, rendering conditions less favourable for native species (Yelenik *et al.*, 2004; Nsikani *et al.*, 2017, 2018a). Because of the fragmented nature of lowland remnants and their proximity to agriculture and other forms of land-use, lowland ecosystems tend to be more disturbed and impacted by a larger suite of alien weed species, especially grasses and forbs (Musil *et al.*, 2005). These aliens become particularly problematic where soil legacy effects persist following alien tree control, and where soil is depleted of fynbos propagules (Yelenik *et al.*, 2004). Mediterranean alien annual grasses (e.g. *Avena fatua*, *Briza maxima*, *Lolium multiflorum*, *Bromus* species) and forbs (e.g. *Echium plantagineum*, *Raphanus rapanistrum*) frequently dominate in highly degraded sites, but may be controlled through appropriate fire management during the restoration process (Petersen *et al.*, 2007).

Riparian zones are more commonly invaded by acacia species (e.g. *Acacia longifolia*, *A. mearnsii*; Holmes *et al.*, 2008) and in the lowland river segments also by eucalypts (especially *Eucalyptus camaldulensis*; Tererai *et al.*, 2013; Ruwanza *et al.*, 2018; Hirsch *et al.*, 2020). Eucalypts are profligate water-users and alter local conditions to create situations of water-repellency and allelopathy in soils, which negatively impacts the ability of native species to persist or establish (Ruwanza *et al.*, 2013; Ruwanza *et al.*, 2015).

The long history of alien plant invasions in the CCS, dating from the 19th century (Wilson *et al.*, 2014), coupled with other intensifying anthropogenic disturbances, means that for some sites a threshold may have been passed beyond which passive restoration by alien clearance alone would be insufficient to restore habitat and ecosystem services (Gaertner *et al.*, 2014). Although the WfW programme was initially optimistic that it could bring alien plant invasions under control and restore ecosystems through spontaneous succession, a quarter century later it is clear that this goal is remote (van Wilgen *et al.*, 2012; van Wilgen *et al.*, 2016b). It is therefore crucial to understand the factors that determine where passive restoration is likely to succeed and to prioritise suitable sites for action before they become degraded to a point where active restoration would be required (Mostert *et al.*, 2018). Furthermore, sites deemed unlikely to self-repair via spontaneous succession need to be reassessed in their landscape context, with a view to defining appropriate restoration goals and associated actions, be they the rehabilitation of a key ecological function or restoration of a diverse native plant community that would be resilient to climate change. Research that informs ecosystem responses to passive and active restoration interventions after alien invasion have, to date, mostly taken place at the field plot scale (Holmes, 2001b; Waller *et al.*, 2016; Hall, 2018). Given the complexities of managing landscapes and the imperative to scale up ecological restoration, insights from research should be applied at a much larger scale at the stage of restoration planning and at all subsequent phases of implementation, within a framework of adaptive management that takes into account factors such as wild fires and re-invasion, as well as social and economic needs.

How to repair the damage: aims of the paper

We review the effectiveness of spontaneous succession in restoring terrestrial and riparian ecosystems affected by alien tree invasions in the CCS, drawing on research and monitoring outputs from the past three decades. We ask: In which situations are the assumptions of spontaneous succession upheld? Are there factors other than intensity or duration of invasion that influence restoration outcomes? Should programmes focussing on mitigating the impacts of plant invasions invest in active restoration interventions that include physical and biotic manipulations after the clearing of alien plants? We conclude with some principles for improving ecological restoration in alien-invaded fynbos ecosystems.

HOW SUCCESSFUL IS SPONTANEOUS SUCCESSION FOLLOWING THE CLEARING OF ALIEN TREES?

The global situation

Some ecosystems degraded by alien plant invasions are able to self-restore through spontaneous succession, provided that the invasion history is relatively recent (Box 2). Examples include tropical forest (Addo-Fordjour *et al.*, 2009), oak woodland (Selvi *et al.*, 2016), arid shrubland (Becerra and Montenegro, 2013), coastal sage scrub (DeSimone, 2011), temperate grassland (Házi *et al.*, 2011) and riparian vegetation (Rubio *et al.*, 2014). Conversely, there are many situations in which active restoration is recommended following alien removal (D'Antonio and Meyerson, 2002). This includes where native seed banks are depleted or if key guilds are missing (Ferreras *et al.*, 2015; Rayburn *et al.*, 2016), and where the surrounding landscape lacks native remnants to serve as source nuclei for seed dispersal (Cerdà *et al.*, 2009; Mucina *et al.*, 2017). Furthermore, where the invasive species have imparted legacy effects and biophysical conditions remain altered post-removal, native species may not establish and active intervention is required (Taylor & McDaniel, 2004; Reisner *et al.*, 2013). In other cases, removal of the invasive species creates space or disturbance that facilitates re-invasion of the targeted alien and/or the incursion and proliferation of secondary alien species (Pearson *et al.*, 2016); re-introduction of native species may be required to pre-empt re-invasion (Reisner *et al.*, 2013). Removal of invasive vegetation may result in soil disturbance which can alter resource availability in favour of other alien species (D'Antonio & Meyerson, 2002). Altered processes following clearing and/or re-invasion, such as a modified fire regime, may also thwart spontaneous succession (Kamo *et al.*, 2002). Land managers therefore need to assess alien-invaded sites in the landscape context as well as at the local (site) scale to assess the degree and types of degradation and the potential impact of alien removal, to determine whether spontaneous succession will occur and thus passive restoration is an appropriate approach.

The Core Cape Subregion

Two decades ago, Holmes and Richardson (1999) postulated that deriving a set of protocols for ecological restoration from the current scientific understanding of fynbos plant community and ecosystem dynamics could improve efficiency of restoration planning and implementation. They developed a conceptual framework and from this a decision tree to clarify situations requiring passive versus active restoration interventions. These were linked to the various protocols according to the perceived degree of degradation. More recently Gaertner *et al.* (2012a) applied the concepts of ecosystem resilience and thresholds in alien-invaded fynbos ecosystems to illustrate how to improve decision-making frameworks. When a threshold is crossed, the reinforcing feedbacks that maintain a system in a certain state change. Biotic thresholds are defined by changes in relative growth form and species composition, whereas abiotic thresholds are defined by alterations of physical processes. Here, resilience is defined as the ability of an ecosystem to recover spontaneously from a perturbation (Westman, 1978), whereas ecosystem thresholds identify break points where the dominance of the regulating processes are replaced by positive reinforcing feedbacks that lead to losses in resilience (Briske *et al.*, 2006). Timpane-Padgham *et al.* (2017) suggested that resilience attributes should form explicit planning objectives at the various scales appropriate to the restoration project to increase restoration success in a changing climate. In alien-invaded vegetation, the crossing of biotic or abiotic thresholds usually indicates loss of resilience and the need for active restoration at a site (Figure 1; Gaertner *et al.*, 2012a), unless the scale of degradation and landscape context can mitigate the loss of that particular biotic or abiotic structure or function. For example, a key biotic structural element initially lost in densely invaded fynbos vegetation is the overstorey proteoid component which lacks soil-stored seeds (Holmes & Cowling, 1997a). For large invaded areas the recommendation is to re-introduce proteoids by seed following alien-clearance and fire. For smaller degraded areas embedded within a natural landscape, however, the biotic threshold may not yet have been passed and colonisation may occur over 1–2 fire cycles through medium-distance dispersal of proteoid seeds into the area after fires (Holmes & Richardson, 1999).

As in all restoration projects, the cause of degradation must first be addressed, in this case through appropriate methods of removing the invasive species (i.e. passive restoration), as the method of control can impact on restoration outcomes. In many cases of alien plant invasion, the first threshold to be crossed is a biotic, structural threshold. This implies that a new guild has established (e.g. trees in a treeless fynbos community) and that, as a result, certain native guilds have been eliminated from the vegetation and seed bank community and would need active re-introduction to restore ecosystem structure. If this scenario is not addressed, the abiotic conditions may change over time, leading to abiotic functional thresholds being crossed. In many invasion scenarios, a stage is reached where biotic and abiotic impacts operate in concert to cause reinforcing feedbacks that promote the alien over the native species, resulting in an alternative stable state (Suding *et al.*, 2004). This has been termed a "biotic-abiotic feedback threshold" by Gaertner *et al.* (2012a) and such a degraded state may be difficult to restore without significant interventions. The above invasion scenario was adapted conceptually as a "three-threshold model" of degradation by Gaertner *et al.* (2012a). This model can be used, with the list of biotic and abiotic ecosystem changes and responses, to assess where thresholds have been crossed and to evaluate whether a passive or active restoration strategy should be implemented, depending on the restoration goal (Figure 1, Table 1). In tandem with the restorative continuum model, the SER has developed a five-star restoration recovery scale, that incorporates four biotic or abiotic structural and functional attributes and two landscape attributes ("external exchanges", i.e. species and gene flows beyond the restoration site, and absence of threats at the restoration site and its adjacent areas; Gann *et al.*, 2019). The latter two attributes will

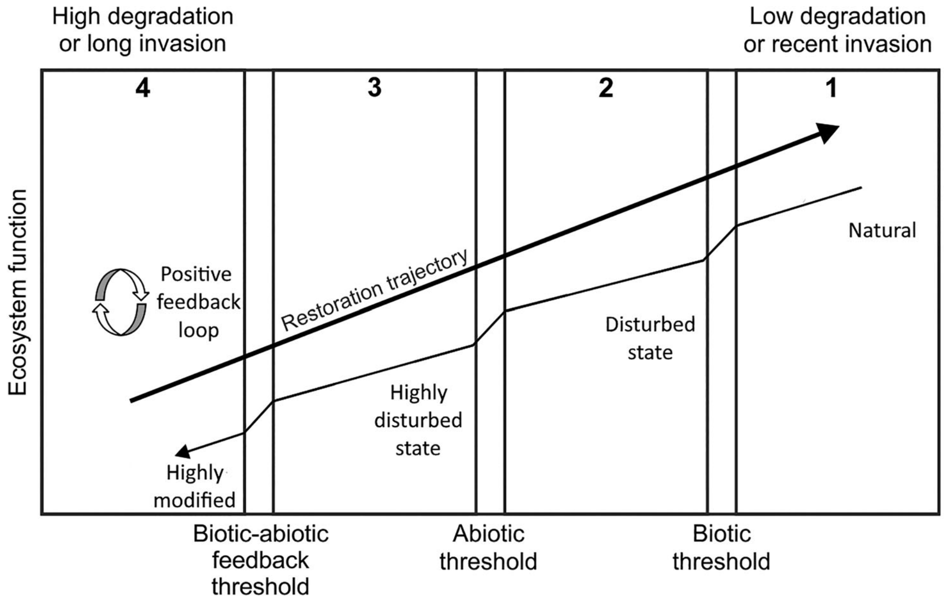

Figure 1. Three-threshold model (after Whisenant, 2002; King & Hobbs, 2006; Gaertner *et al.*, 2012a; Holmes *et al.*, 2020) illustrating the concept of thresholds which indicate break points between alternative ecosystem states. (1) Natural ecosystem state: no threshold reached and spontaneous succession following alien control is a viable strategy. (2) Disturbed ecosystem state: biotic threshold is reached; key disturbance (KD) structural factors include increased invader biomass, seed production and dominance of alien seedlings; key response variables (KRV) include altered native community structure, seed bank, declines in functional groups and species richness. Active re-introduction of any depleted key native structural or functional groups is required. (3) Highly disturbed ecosystem state: biotic and abiotic thresholds are reached: In addition to (2), KD factors include altered soil nutrient and water availability, and increased competition for resources; KRV include further loss of native species and functional groups. Soil factors (e.g. excess nutrients) may need amendment prior to active re-introduction of native structural and functional groups. (4) Highly modified alternative stable ecosystem state: positive feedbacks trigger threshold to be reached whereby KD functional factors, such as allelopathy, altered microbial systems and fire regime, entrench dominance of invasive alien species at the expense of native species. A less ambitious restoration goal may be required. In alien-invaded fynbos, the break points usually link to fires which trigger the reassembly of plant communities.

affect long-term sustainability of a restoration project and should be considered when setting restoration goals.

Ecological features of fynbos that influence the spontaneous succession response

As fynbos vegetation is fire-prone and fire-dependent, species have evolved life-history traits to persist under this disturbance regime, either by resprouting after fire or regenerating from seed banks stored in the canopy or soil. In natural vegetation, resprouting shrubs, graminoids and geophytes dominate the initial post-fire cover, yet around 50% of fynbos species are killed by fire, and most species regenerate from persistent soil-stored seed banks (Holmes & Richardson, 1999). Fynbos is similar to tropical grassland ecosystems in being resilient to the endogenous fire disturbance regime yet vulnerable to soil disturbance (Buisson *et al.*, 2019), particularly ploughing which destroys below-ground structures such as lignotubers, bulbs and seed banks (Joubert *et al.*, 2009). Fynbos riparian vegetation comprises a variety of plant communities, which can be fire-adapted, with the dominant fynbos riparian scrub species mostly being resprouters (Prins *et al.*, 2004). An exception is riparian forest communities that include non-fire adapted Afrotemperate Forest species. These forest communities are mostly confined to fire refuges, such as under cliff faces, on boulder screes or along streams in rocky ravines.

Fires occur mainly in the dry season, which is in summer for the Mediterranean-climate, western portion of the CCS. Seeds are cued to germinate either directly by fire (following exposure to a heat pulse or smoke chemicals) or indirectly, for example by detecting changes in diurnal temperature amplitude following removal of insulating vegetation cover (Kraaij & van Wilgen, 2014). In ecological management it is important to implement a natural fire regime (including frequency, season and intensity), if necessary by prescribed burning, to maintain diversity, community structure and ecosystem function. The feasibility of using prescribed burning as a restoration tool in alien-invaded degraded fynbos will depend on the extent of degradation caused, characteristics of the alien invader and whether native seed banks persist. As a general recommendation, where dense invasion is recent (i.e. dense only since the last fire) and fynbos seed banks are expected to persist (Holmes & Cowling, 1997a; Holmes, 2002), a prescribed burn after clearing of the invasive stand should initiate spontaneous regeneration by stimulating germination of dormant fynbos seeds in the following wet season. However, there are exceptions where fire could negatively impact on ecological restoration following alien clearance, as discussed below.

For passive restoration to succeed in fynbos ecosystems, either some native vegetation must persist under the aliens, or soil-stored seed banks should have remained relatively intact. This is because typical dispersal distances are very short (in the order of a few metres by ant, passive or ballistic dispersal) with wind dispersing some species further, though even those are mainly trapped locally by vegetation (Holmes

Table 1. Examples of dense invasion scenarios in the Core Cape Subregion, with assessed degradation impacts in relation to biotic and abiotic thresholds (see Figure 1) and passive and active interventions that are required to restore ecosystem structure and functioning. A, pine invasion (*Pinus pinaster* and *P. radiata*) in mountain fynbos; B, acacia (*Acacia saligna*) invasion in lowland fynbos; C, acacia invasion (*Acacia longifolia* and *A. mearnsii*) in mountain stream and foothill riparian ecosystems; D, eucalypt invasion (*Eucalyptus camaldulensis*) in lowland riparian ecosystems. Some case studies are also shown as decision trees (Figure 2) or photographic panels (Figure 3); Table 2 outlines alternative passive restoration methods.

Duration dense invasion >70% projected canopy cover	Threshold			Restoration interventions		References
	Biotic	Abiotic	Biotic/abiotic feedback	Passive	Active	
A. Pine invasion in mountain fynbos (see also Figure 2A and Figure 3A)						
<1 fire-cycle	No: Soil seed banks intact; resprouters and proteoids still persist	No: Reduced soil water will recover with pine clearance; pine litter is acidic as in fynbos and slow to change soil chemistry	None at this stage	Clear by felling trees. If fuel loads low (i.e. <10 year-old stand) burn 1–2 years later in summer. Where fuel loads very high, extract timber prior to burning. Regular follow-up of pine saplings will be required	Not required; spontaneous succession adequate	(Holmes & Marais, 2000) (Mostert *et al.*, 2017)
1–2 fire-cycles (10–30 years of dense invasion)	Shift in vegetation structure: increased biomass by alien; loss of overstorey proteoid layer; reduced fynbos seed production and soil seed bank density and diversity	Reduced water availability; increased biomass could lead to increased fire severity	No: provided that severe wild fire avoided that could kill native propagules and trigger soil erosion	As above; a wet season fuel reduction burn may be advised where felled biomass at soil surface is high, to circumvent a damaging summer wild fire	Overstorey proteoid component to be re-introduced by seed following fire where invaded area is extensive (>0.5 km diameter); sufficient seed banks remain to re-instate structure	(Richardson & Van Wilgen, 1986) (Holmes *et al.*, 2000) (Holmes, 2001a) (Galloway *et al.*, 2017)
>2 fire-cycles (>30 years)	Altered vegetation structure with pine trees dominating. Only short-lived (<5 year) fynbos components persist through rapid post-fire seed bank replenishment ahead of pine canopy closure; slower-growing fynbos species eliminated and seed banks depleted	As above	Loss of native propagules leads to decreased resilience post-fire; severe soil erosion could result	Fell pines and remove large timber where feasible; alternatively, a wet season burn may be prescribed to reduce biomass and pre-empt damaging summer wild fire. A further alternative is to burn pines standing; but note this will result in massive seed release from cones and either intensive manual follow-up or a second prescribed burn ahead of pine reproductive maturity	Once pines are removed and the site burnt, a comprehensive fynbos seed mix, comprising all major growth forms, should be sown in autumn; the resprouter component may need to be augmented by planting rooted material; anti-soil erosion measures should be adopted in vulnerable areas ahead of winter rains	(Richardson & van Wilgen, 1986) (Galloway *et al.*, 2017)
Note: Pine invasion in lowlands as above, except that a biotic threshold reached sooner than in mountains owing to lower persistence in seed banks compared to mountain fynbos ecosystems.						(Petersen *et al.*, 2007); (Mostert *et al.*, 2017)

(*Continued*)

Table 1. Continued.

Duration dense invasion >70% projected canopy cover	Threshold			Restoration interventions		References
	Biotic	Abiotic	Biotic/abiotic feedback	Passive	Active	
B. *Acacia* invasion in lowland fynbos (see also Figure 2B and Figure 3C)						
<1 fire cycle (<20 years of dense invasion)	Shift in vegetation structure: increased biomass by alien; loss of overstorey proteoid layer; reduced fynbos seed production and soil seed bank density and diversity	Increased soil N and pH; reduced water availability	Increased competition for resources; suppression of native species	If >10% cover of multiple fynbos guilds present, Fell & Stack alien slash and allow fynbos to recover before burning site; continue with follow-up alien control, but minimise herbicide use	Prescribed summer burn once fynbos species have matured and replenished seed banks; re-introduce missing guilds post-fire; continue alien follow-up control	(Holmes, 2002) (Mostert *et al.*, 2017) (Krupek *et al.*, 2016) (Nsikani *et al.*, 2017) (Hall *et al.*, 2017) (Hall, 2018)
1–2 fire cycles (>20 years of dense invasion)	Altered vegetation structure with alien acacia dominating. Few fynbos species evident in above-ground vegetation; fynbos soil seed banks depleted with only a few short-lived species represented; acacia has high seed bank density, maintaining granivores	Reduced water availability; increased biomass leads to increased fire severity; increased soil N and pH	Altered nutrient cycling patterns, microbial communities and fuel bed characteristics create positive feedbacks whereby dominance of the invader is entrenched at the expense of native species	Combine passive methods with active restoration otherwise aliens will continue to dominate. Fell & Stack acacia and maintain follow-up control, particularly after fire; or Fell & Burn slash 2 years later; control granivores by erecting owl boxes and raptor perches; control domestic livestock grazing with fencing until vegetation well established	Sow a comprehensive fynbos seed mix on bare soil between stacks, or after delayed burn; pre-treat seeds with smoke and heat shock as required; plant rootstock of guilds difficult to re-introduce by seed, such as obligate fynbos resprouters; re-introduce missing guilds after subsequent fires; burning removes nutrient-rich litter	(Slabbert *et al.*, 2010) (Nsikani *et al.*, 2018b) (Nsikani *et al.*, 2018a) (Hall, 2018)
Note: Where fynbos seed banks are absent an alternative goal to ecological restoration should be sought to prevent re-invasion by alien plants and reduce costs, unless the site represents critically endangered habitat and is required for the re-introduction of threatened plant species.						
C. Acacia invasion in mountain stream and foothill riparian reaches (landscape scale processes remain intact unless impacted by aliens; see also Figure 3D)						
<1 fire cycle (<20 years of dense invasion)	Shift in vegetation structure: increased biomass by acacia; loss of some fynbos riparian scrub species; reduced cover of riparian scrub; high acacia seed production	Soil N may increase, but threshold not crossed in most cases	No	Clear using Fell & Remove method; or reduce alien fuel by killing trees standing or burning slash in stacks on bare ground areas; minimise herbicide use; prevent fires until riparian scrub is recovered; ensure follow-up control	None required in 95% of cases if best practice passive methods applied, as riparian scrub structure recovers spontaneously; propagules may colonise from upstream remnants	(Blanchard & Holmes, 2008) (Reinecke *et al.*, 2008) (Vosse *et al.*, 2008)

(*Continued*)

Table 1. Continued.

Duration dense invasion >70% projected canopy cover	Threshold			Restoration interventions		References
	Biotic	Abiotic	Biotic/abiotic feedback	Passive	Active	
1–2 fire cycles (>20 years of dense invasion)	Shift in vegetation structure: total dominance of acacia and increased stand biomass; loss of fynbos riparian scrub except the most shade-tolerant species; large acacia soil-stored seed bank and diminished native seed bank	Reduced water availability; altered bacterial communities, increased soil N; increased N and P in river sediments; altered fuel bed characteristics promoting severe fires	Increased competition for resources; increased soil N and altered nutrient cycling patterns create positive feedbacks whereby dominance of the alien is entrenched at the expense of native species	Fell & Remove alien biomass or fell in strips (4-stage method) stacking biomass outside riparian zone; ensure follow up control of aliens	Propagate rootstock of dominant fynbos riparian scrub species; sow scrub species in autumn and/or plant rooted material in winter/ spring; wet bank species should recolonise from upstream; prevent fires until native species are well established	(Fourie, 2008) (Pretorius *et al.*, 2008) (Reinecke *et al.*, 2008) (Slabbert *et al.*, 2014) (Crous *et al.*, 2019) (Strydom *et al.*, 2017)
D. Eucalypt invasion in lowland river riparian reaches (landscape scale processes often modified by surrounding land uses and upstream impoundments, thus rehabilitation is maybe a more realistic goal; see also Figure 2C and Figure 3E)						
<30 years	Shift in vegetation structure: increased biomass by alien; loss of fynbos riparian scrub and tree species; reduced cover and seed bank of native species	Reduced water availability; increased shading, soil water repellency and allelopathy	Increased competition for resources; suppression of natives except most shade-tolerant, hardy species	Fell & Remove timber; clear aliens in strips (4-stage method); ensure follow-up control	Propagate rootstock of dominant fynbos riparian scrub and tree species; plant rooted material in cleared strips in winter/spring; where geo-morphology remains natural consider also sowing natives and re-introducing wet bank species	(Ruwanza *et al.*, 2013, a,b,c) (Tererai *et al.*, 2013) (Ruwanza *et al.*, 2015) (Tererai *et al.*, 2015a) (Tererai *et al.*, 2015b)
>30 years	Vegetation structure dominated by large eucalypt trees; high alien biomass and seed production; large declines in functional groups and species richness	Reduced water availability; intensified shading, soil water repellency and allelopathy	Positive feedbacks entrench dominance of eucalypts	Fell & Remove timber; clear in strips (4-stage method); ensure follow-up control	Propagate rootstock of dominant fynbos riparian scrub and tree species, including bird pollinated and dispersed species; plant rooted material in cleared strips in winter/ spring; in highly modified reaches, non-invasive alternatives may be planted for revegetation purposes	(Geldenhuys, 2013) (Geldenhuys *et al.*, 2017) (Mangachena & Geerts, 2017)

& Richardson, 1999). Thus for many species, dispersal into a degraded site from the surrounding landscape will be extremely slow, unlike in tropical forest ecosystems where vertebrates initiate spontaneous succession by importing seeds from surrounding forest patches (Holl & Aide, 2011). Riparian ecosystems have the advantage of hydrochory as a mechanism for spontaneous succession, with some propagules able to disperse downstream from natural remnants higher up in the catchment (Galatowitsch & Richardson, 2005), while herbaceous species and low understorey shrubs are represented in the soil-stored seed bank (Vosse *et al.*, 2008).

Four main factors influence the ability of an invaded fynbos plant community to recover through spontaneous succession, namely: density of invasion, duration of invasion, species of invader and major ecosystem type (particularly mountain versus lowland fynbos types). We review research in relation to these four factors that has been conducted in fynbos terrestrial and riparian ecosystems. The method and efficacy of alien control applied also influences the outcomes; this also is discussed below.

The density of invasive tree stands

Alien trees spread into fynbos vegetation as invasive fronts or nascent foci, the rate of invasion depending on the species' seed dispersal characteristics and fire frequency; successful alien species in fynbos are fire-adapted (Wilson *et al.*, 2014). Fynbos species can survive under the aliens until the projected alien canopy cover exceeds about 70%, after which species die off owing to shading or other competitive effects. Even where fynbos species persist, the alien may negatively impact on their ability to flower or set seed, to the extent that seed banks fail to be replenished and local species extirpation can occur after the next fire. This is especially the case for serotinous species that have no buffering soil-stored seed banks. However, in most cases of less dense invasion, sufficient fynbos or fynbos seed banks persist to allow for spontaneous succession after alien removal (Holmes & Cowling, 1997a). In riparian vegetation the same applies, although there is a higher component of native species in headwater streams that resprout after fire (Prins *et al.*, 2004), tolerate shading (e.g. thicket resprouters) and may persist longer with invasion than is the case in terrestrial fynbos. In foothill and lowland rivers, *Eucalyptus camaldulensis* caused a consistent decrease in species richness and diversity along an invasion gradient (Tererai *et al.*, 2013).

The duration of dense invasive tree stands

Once the invasion becomes dense, a monoculture develops, with fewer species and growth forms surviving in the aboveground vegetation. Some fynbos resprouter shrubs and graminoids persist longer than obligate reseeder species, possibly owing to underground resources that maintain their carbon balance. In mountain fynbos ecosystems on the Cape Peninsula, Holmes & Cowling (1997a, b) found that fynbos species richness, cover and frequency all declined in above-ground vegetation occupied by dense acacias that had been present for 1, 2 or more fire cycles. However, changes in soil seed bank composition lagged behind this and indicated good potential for spontaneous succession post-fire after 1–2 fire-cycles of dense invasion. In some sites where dense stands of invaders had been present for many decades some growth forms persisted in the seed bank at very low densities and frequencies, conferring lower restoration potential. Here colonisation by bird-dispersed thicket resprouters occurred at some sites under the acacias, further altering vegetation structure as these are not typical fynbos elements except in fire refugia (Holmes & Cowling, 1997b). Following recent, dense pine invasion in the mountains, spontaneous succession returned all growth forms and >80% of species after alien clearance and fire (Holmes & Marais, 2000). This is considered "5 star restoration" by the SER (Gann *et al.*, 2019). However, for older cleared pine plantation areas with mixed acacia invasions in another mountain catchment area, spontaneous succession was less successful, resulting in lower vegetation cover and 65% species richness compared to the reference site (Fill *et al.*, 2017).

In cleared pine plantations in the lowlands Mostert *et al.* (2017) found fynbos recovered well in terms of indigenous perennial species richness, but indigenous species cover decreased with increasing number of planting rotations. In mountain fynbos following pine forestry, Galloway *et al.* (2017) found that the threshold to recovery by spontaneous succession lay between 30 and 50 years based on post-fire recruitment and persistent soil seed banks in harvested pine compartments of those ages. In most cases, serotinous fynbos species were the first guild to be locally extirpated by dense invasion; re-introduction would be required in situations where no adjacent subpopulations are present to recolonise.

There are no comparable data for duration of dense invasion impacts in riparian vegetation. However, our observations in headwater streams suggest that native trees and resprouting thicket shrubs are the growth forms that persist longest; some herbaceous species persist along the edge of the wetbank zone where there is good light penetration.

Identity matters: different invasive species = different problems

The variable impact of different invasive alien tree species on fynbos restoration potential can be attributed to their growth form and life-history characteristics. For example, comparing acacias with pines: the former grow much more rapidly from seed and in new dense stands can overtop and shade out the fynbos community within one year, whereas canopy closure in invasive pine stands can take up to seven years. The implications of these differential growth rates are that in acacia stands only the very short-lived fynbos species have time to flower and set seed to replenish their seed banks before being outcompeted. In pine stands a larger diversity of species and growth forms can reproduce and persist. Acacias fix atmospheric nitrogen which improves their productivity, growth and competitive ability in nutrient-poor ecosystems such as fynbos. As the duration of dense invasion increases, ecosystem-level changes occur. Under acacia, soil pH, nitrogen (N) and phosphorus (P) increase but under pine few changes have been observed (Mostert *et al.*, 2017). Several studies indicated that *Acacia saligna* enriches fynbos soils (Yelenik *et al.*, 2004; Gaertner *et al.*, 2011; Nsikani *et al.*, 2017). One study showed that *Eucalyptus* greatly increased leaf litter and soil micro-nutrient concentrations compared to reference fynbos, whereas Kikuyu grass (*Pennisetum clandestinum*) invasion caused no significant soil changes (Gaertner *et al.*, 2011). Such soil changes can persist and cause a reinforcing positive feedback loop (Figure 1) benefiting the alien and potentially leading to an alternative stable state (Gaertner *et al.*, 2012a). Nsikani *et al.* (2017) consider these changes a legacy effect of invasion, as raised pH and NO_3^- levels were found to persist for 10 years after alien clearance. Often these ecosystem-level changes are matched by biotic changes; for example Mostert *et al.* (2017) found species richness declined more under acacia than under pine. In cleared, long-invaded acacia stands, secondary invasions by alien herbaceous grasses or forbs and native grasses that benefit from soil nutrient enrichment is a likely scenario that could pose a barrier to active restoration initiatives (Yelenik *et al.*, 2004; Nsikani *et al.*, 2017).

In terms of life-history, acacias produce a legacy of long-lived seeds that accumulate in the soil seed bank (Strydom *et al.*, 2019) whereas pines are serotinous and store seeds in the canopy. Pines can be eliminated by felling followed by one prescribed burn to kill seedlings, whereas for acacias a portion of the seed bank remains dormant after a fire. Consequently, acacia control generally requires many more follow-up clearing sessions than is the case for pines, making restoration more expensive. Species like *Acacia saligna* have heat-stimulated seeds and also resprout vigorously after fire (Hall *et al.*, 2017). This combination of traits makes *A. saligna* very difficult to control without skilled use of herbicides, further adding to the costs. Unfortunately, herbicide use, even if applied carefully and only on cut stumps, has a negative impact on spontaneous succession as a result of chemical drift inadvertently killing native species (Krupek *et al.*, 2016).

Biological control has been applied to many invasive alien plants in South Africa, including acacias, but so far not for pines due to concerns of commercial impact. For example, the fungus *Uromycladium tepperianum* produces copious galls on *Acacia saligna*, greatly reducing the growth, vigour and life-span of the tree (Wood & Morris, 2007). In the early part of an invasion front this has the important impact of slowing growth and maintaining an open alien canopy, thereby reducing shading and other competitive effects of the alien on fynbos species, promoting their co-existence and enhancing the feasibility of spontaneous succession achieving the aims of restoration. Furthermore, several introduced seed-destroying *Melanterius* weevils have been introduced as back-up biological control agents on acacias whose impacts are argued to accrue over time and reduce the species' reproductive fitness (Impson & Hoffmann, 2019). Nevertheless, acacias in dense monospecific stands where seed agents are present still accumulate stand-replacing seed banks (Strydom *et al.*, 2019). It will take time, possibly several fire cycles, before the legacy of large seed banks of acacias can be significantly reduced, and follow-up alien control will remain an essential long-term component of any restoration strategy for the foreseeable future.

In riparian ecosystems, acacias also have a legacy of enriching soils and accumulating large stores of persistent seeds in the soil (Le Maitre *et al.*, 2011; Crous *et al.*, 2019). Another legacy noted following acacia control was the persisting higher levels of damage by phylopathogenic fungi and folivorous insects on two native riparian trees, despite the recovery of riparian scrub vegetation by spontaneous succession (Maoela *et al.*, 2016). Soil bacterial communities were found to change under acacia, but reverted to those of fynbos riparian scrub following passive restoration (Slabbert *et al.*, 2014). In lowland rivers, *Eucalyptus* was found not to significantly modify soil macro-, micro- and available nutrients (Tererai *et al.*, 2015a). Although *Eucalyptus* increased soil water repellency at some sites, this effect did not persist after clearing (Ruwanza *et al.*, 2013). However, *Eucalyptus* produces allelopathic chemicals from roots and bark that inhibit germination and growth of some native species (Ruwanza *et al.*, 2015) and this impact could lower spontaneous succession potential.

Ecosystem type

Another factor that influences the feasibility of spontaneous succession to restore invaded fynbos is the type of ecosystem invaded. This difference was not anticipated but came to light during a seed bank study incorporating mountain and lowland fynbos ecosystems invaded by *Acacia saligna* (Holmes, 2002). There was lower persistence of fynbos seeds in the soil seed bank of lowland compared to mountain fynbos and much lower persistence of the longer-lifespan reseeder species component in lowland fynbos. The dominance of short-lived herbaceous species in seed banks of invaded lowland fynbos indicates that spontaneous succession would result in a herbland rather than a shrubland. Both fynbos ecosystems support similar plant taxa, with fire-related recruitment traits, so the difference in seed bank persistence may be the result of much higher fossorial mammal disturbance and granivore activity observed in lowland fynbos, which likely reduces both seed inputs and survival in the soil. Acacias provide food for granivores via annual seed fall, thus maintaining their populations to further reduce fynbos seed survival in the lowlands. Although acacias are the major invaders in lowland fynbos, it was observed in a lowland pine plantation that small mammals were largely absent (Rebelo *et al.*, 2018), which may partly explain why seed banks persist better under pines compared to acacias in these ecosystems.

Method and efficacy of invasive tree control

Initial clearing methods for alien tree control in fynbos are Fell Only (in threatened lowland ecosystems slash is often stacked, then left to rot or stacks burnt in winter) and Fell & Burn (usually with burning in autumn if fuel loads are low, or burning in winter/spring if fuel loads are high) (Table 2). The Fell & Burn method is almost never used owing to the South African legislative environment which places responsibility for any negative impact of a fire on the person igniting that fire (National Veld & Forest Fire Act 101 of 1998, Government Gazette Volume 401, No. 19515). This has led to situations of litigation despite the fact that failing to clear the aliens or burning felled slash could be considered irresponsible as high fuel loads could lead to a dangerous wild fire. Another method is Burn Standing: although seldom used it is potentially cost-effective and results in fewer negative impacts on soil and seed banks because fuel is held higher off the ground. However, Burn Standing requires the alien-dominated vegetation to be dry and the conditions suitable for a summer burn, with the same risks implied as for the Fell & Burn method. A fourth method used is Kill Standing, either by ringbarking or frilling the trees. This method is appropriate for strongly root-suckering species such as *Acacia melanoxylon* and *Populus* x *canescens*. Where dense stands are extensive or inaccessible by foot, trees sometimes are foliar-sprayed with herbicide from helicopter or boom-sprayer; however such treatment may negatively impact on fynbos recovery (Parker-Allie *et al.*, 2004). To reduce felled fuel loads and minimise damage to soils and seed banks in a dry season wild fire, the larger wood may be removed and sold to industry (for wood chip, poles or sawmill timber as appropriate) (Theron *et al.*, 2004). The utilisation of alien plant biomass, where it is done (for example the widespread utilisation of *Acacia cyclops* for firewood) should ideally be closely integrated with control efforts, but there is no evidence (for example in management plans) that this is currently done. This Fell & Remove method is not economically viable in remote or inaccessible areas. As discussed above, the Fell & Burn method successfully restores fynbos where fuel loads are relatively low (Holmes & Marais, 2000; Holmes *et al.*, 2000). Alternatively, denser felled slash – either in stacks or across the site – may be burnt during the cooler season while soils remain wet, to minimise damage to soils and seed banks (Holmes 2001a). This may not result in optimal spontaneous succession if germination cues of native species are not met or if post-fire conditions in Spring are less suitable for establishment compared to the Autumn/Winter season following a summer/dry season prescribed burn (Holmes, 2001a).

In lowland fynbos invaded by acacias, the use of fire may be a double-edged sword. Fire is needed to stimulate any residual fynbos seed banks in the soil, burn off the nutrient-rich litter and (usually) create a seed bed for active restoration, but simultaneously this stimulates mass germination of the heat-stimulated acacia seeds. Invariably this leads to herbicide spraying being used in follow-up control with the negative impacts this implies for any recruiting fynbos species (Krupek *et al.*, 2016). The alternative method of Fell & Stack results in a bare landscape devoid of fynbos or acacia germination, leaving the area open to secondary invasion by weedy herbaceous species (Hall, 2018; Nsikani *et al.*, 2019). Where acacia seed banks are known to be relatively small, the Fell & Burn treatment works well to promote the spontaneous succession of fynbos species from the seed bank. This was observed for lowland fynbos following three successive rotations of pine plantations and a Fell & Burn treatment where it was feasible to remove acacia seedlings manually (Petersen *et al.*, 2007). In contrast, for lowland fynbos invaded by dense acacias, spontaneous succession is unlikely to be sufficient to restore fynbos structure and function. Owing to the challenges resulting from the commonly applied control methods, alternative alien control methods have been proposed for trial in areas of high conservation importance (Hall, 2018). These include a Fell & Burn method with delayed burning (by two years) followed by fynbos sowing, as it was found that acacia seed banks declined by 80% within two years of initial clearance; and a Fell & Stack method with active fynbos sowing to pre-empt or reduce secondary invasions in the bare soil areas.

In riparian vegetation along headwater and foothill reaches, Blanchard and Holmes (2008) found that the Fell & Remove method resulted in better regeneration than Fell & Burn or Fell Only methods. Burning with high fuel loads at the soil surface may kill fynbos seed banks while stimulating mass germination in heat-stimulated acacias. In lowland riparian zones invaded by *Eucalyptus* both clear fell and thinning methods promoted recovery along a trajectory towards native community structure and composition, but it was recommended that a four-stage thinning process would optimise spontaneous succession where a native tree stratum is the goal (Geldenhuys & Bezuidenhout, 2008; Ruwanza *et al.*, 2013a).

In terms of follow-up control for resprouting alien trees, the use of herbicides should be minimised if the goal is to restore ecosystem composition, structure and function. Foliar spraying had the highest negative impact on native species richness, followed by the cut and herbicide-stump method when compared to the non-herbicide method of cutting plants below the root crown (Krupek *et al.*, 2016). The last method is the best from a restoration perspective, but the most expensive; it is therefore only feasible where recruitment of resprouting alien trees is low.

Research on the efficacy of alien plant management has highlighted the need to differentiate between the resources required to achieve the management goals for alien control and the skill levels attained in applying the intervention (Cheney *et al.*, 2019). Using 20 years of data from the Table Mountain National Park, Cheney *et al.* (2019) modelled that to achieve a management goal of <1 acacia plant/ha across the entire park would take between 32 and 42 years, assuming 100% efficacy of control methods. However, when current efficacy levels (80%) were used over 50 years, the model predicted that only 53% of areas would achieve this goal. New seed inputs from standing acacias were found to be more important drivers of persistence than fire-stimulated germination from acacia soil-stored seed banks. The authors concluded that increasing financial resources for acacia control would have little value unless the effectiveness of control methods is increased. Given the negative impact of herbicides used in acacia follow-up control (Krupek *et al.*, 2016), poor initial clearance efficacy will have the added disadvantage of further reducing restoration effectiveness through spontaneous succession.

Returning to our key questions, first: In which situations are the assumptions of spontaneous succession upheld? Essentially, at sites where a biotic or abiotic threshold has not yet been crossed following alien invasion, spontaneous succession is a viable restoration strategy. Thus, diverse growth forms of fynbos either should survive in aboveground vegetation of the alien stand, or the soil-stored seed bank should be sufficiently diverse and abundant to regenerate a structurally-representative fynbos community post-fire. In most cases of recent, dense alien invasion (<2 fire-cycles, or <30 years) spontaneous succession can be assumed. However, lowland fynbos invaded by dense acacia is an exception, because seed banks of longer-living fynbos species decline rapidly following invasion. For such lowland sites, a change from passive to active restoration approaches would be indicated when the cover of diverse fynbos growth forms that persist under an acacia canopy falls below 10% (Hall, 2018). Four of the main invasion scenarios described in this section, and the applicability of spontaneous succession to restoration, are outlined as decision trees (Figure 2 A–C) and/or in the photograph panels (Figure 3 A–E).

Secondly: Are there factors other than intensity or duration of invasion that impact on restoration outcomes? The cases reviewed in this paper show that both the species of alien invader and the ecosystem type affect the feasibility of passive restoration as a management strategy. In general, acacias and eucalypts have a higher impact on fynbos ecosystems than do pines or hakeas; this means that biotic and abiotic thresholds are crossed sooner and the duration in which spontaneous succession operates is shorter under acacias or eucalypts once alien stands become dense. Comparing ecosystems, lowland fynbos is more rapidly degraded by invasion than mountain fynbos owing to lower native seed bank persistence. Ideally, all alien control methods should be applied skilfully to optimise outcomes and minimise any negative impacts on native species. Unfortunately, this cannot be

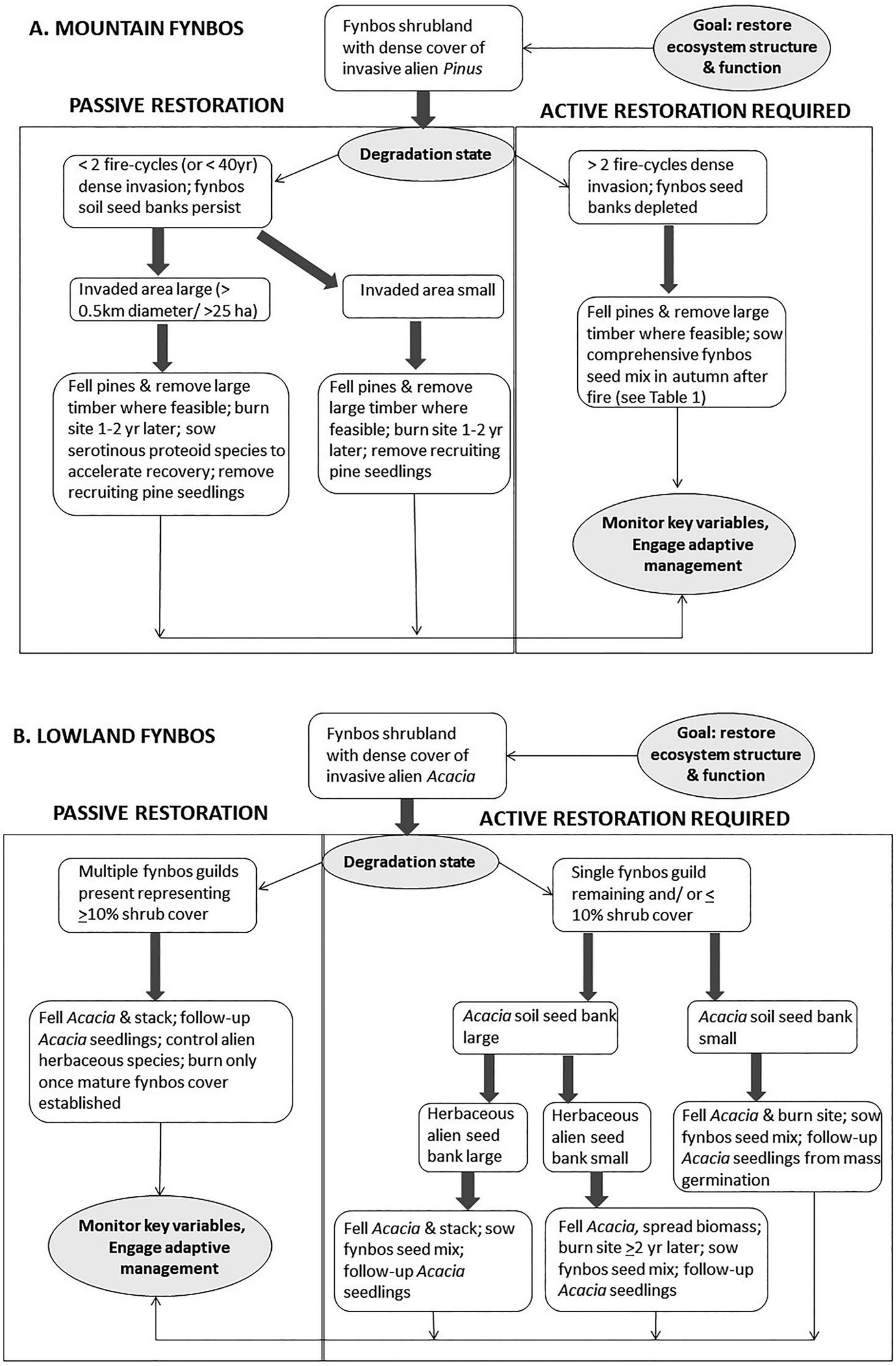

Figure 2. Decision trees for restoring invaded ecosystems using case studies from the Core Cape Subregion, indicating where passive restoration, which relies on spontaneous succession, is an appropriate strategy. Further details are outlined in Table 1 and Figure 3. A. Mountain fynbos invaded by dense pines. B. Lowland fynbos invaded by dense acacias. C. Lowland riparian ecosystems invaded by dense *Eucalyptus*.

guaranteed and the efficacy of the clearing method is thus another crucial factor that may impact on restoration outcomes and the viability of spontaneous succession.

Thirdly: Should restoration programmes invest in active restoration interventions such as physical and/or biotic manipulations after alien clearance? In an ideal world the answer to this question would be "yes" for all situations in which spontaneous succession cannot be relied upon: recent global and national targets for ecological restoration require that current initiatives should be significantly scaled up in an effort to mitigate climate change and build resilience into natural ecosystems. However in real-world situations at local scale, land managers must weigh up the extra cost of active restoration compared to using limited resources to control further invasions. The most important issue that confronts managers is whether or not active restoration would be affordable. This

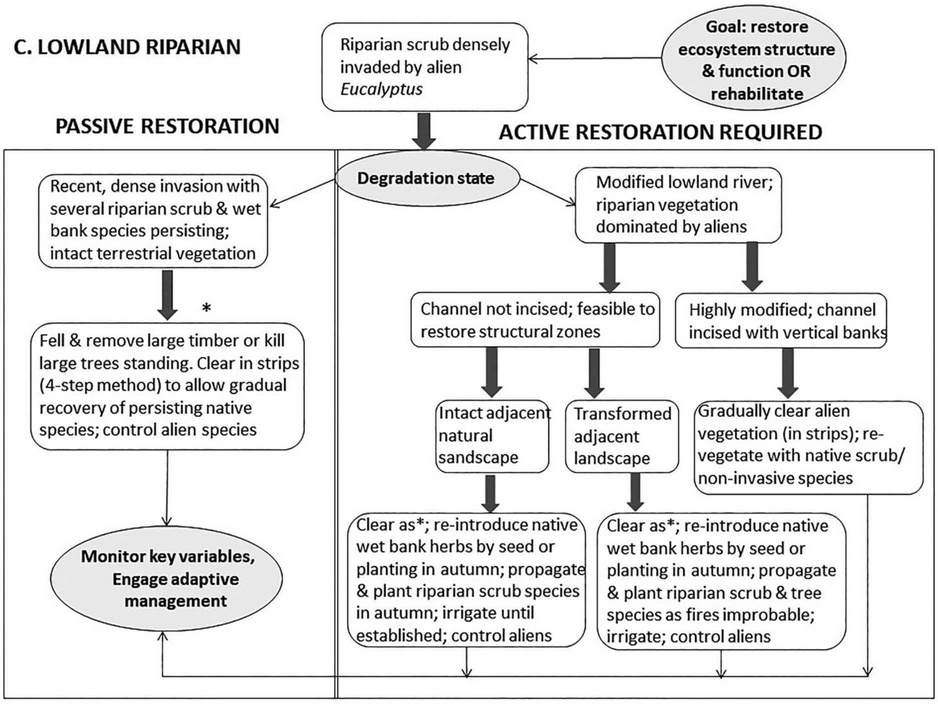

Figure 2 *Continued*

in turn will depend on several factors, including the resources (money and skilled workers) that realistically would be available, and the value of the target ecosystem itself. There are several situations where it would potentially be important to implement active restoration actions after initial clearing measures have been undertaken:

1. In highly degraded ecosystems that protect vital ecosystem services, where taking no action would result in re-invasion by the targeted alien species or secondary invaders, leading to a reduction in the relevant services and undermining the initial investment in alien control.
2. Where alien clearance leaves an unstable substratum that would be prone to erosion and topsoil loss without stabilisation and revegetation. Such further degradation could result in expensive downstream impacts (e.g. siltation of dams, infrastructure damage) and incur high costs to reverse.
3. In threatened ecosystems where insufficient natural remnant area remains to meet minimum conservation targets: this invariably applies to lowland fynbos and renosterveld ecosystems.
4. Where social or economic analyses indicate additional benefits to actively restoring key components, e.g. proteoid and ericoid shrubs that support the cut flower and tourism industries (e.g. Gaertner *et al.*, 2012b).

In the next section we summarise the recommended active restoration approaches for highly degraded lowland and mountain fynbos and in riparian ecosystems.

ACTIVE RESTORATION APPROACHES IN HIGHLY DEGRADED INVADED SITES

Sites assessed to have low potential for spontaneous succession will require active restoration interventions to meet rehabilitation or restoration goals (Figure 2 A–C). As discussed above, these will be densely invaded sites where biotic and/or abiotic thresholds to recovery have been crossed. The protocols outlined by Holmes and Richardson (1999) still broadly apply in terrestrial fynbos, but the research reviewed above has highlighted some nuances in terms of species of alien, ecosystem type and efficacy of initial and follow-up control that should be taken into account when assessing whether active restoration is required. In densely invaded riparian vegetation, alien species also impact on spontaneous succession potential, as does the landscape position: whether mountain stream or lowland river. In all cases, the landscape context, particularly the impacts of adjacent land-use, can influence spontaneous succession potential and the interventions required.

Owing to the high beta and gamma diversity of fynbos communities, active restoration through seeding and planting requires local material to be collected for each project to conserve local gene pools and biodiversity (Holmes & Richardson, 1999) (Table 3). Furthermore, to return representative species composition often requires a significant proportion of locally rare species that may be difficult and expensive to source. For these reasons, it is pragmatic for active restoration interventions to set a goal that prioritises ecosystem structure and function, through returning a diversity of representative common species in each major structural and functional guild. Following dense alien invasion of natural vegetation, the initial goal generally would be “three star” or “four star” restoration, with potential in the longer term to aim for “five star” restoration (Gann *et al.*, 2019), by post-fire re-introductions of any key missing elements, the rarer species, and targeting nature conservation areas or populations of any threatened species that may have become locally diminished.

Mountain fynbos

In most examples of mountain fynbos the context is one of extensive and contiguous fynbos stands, such that dense

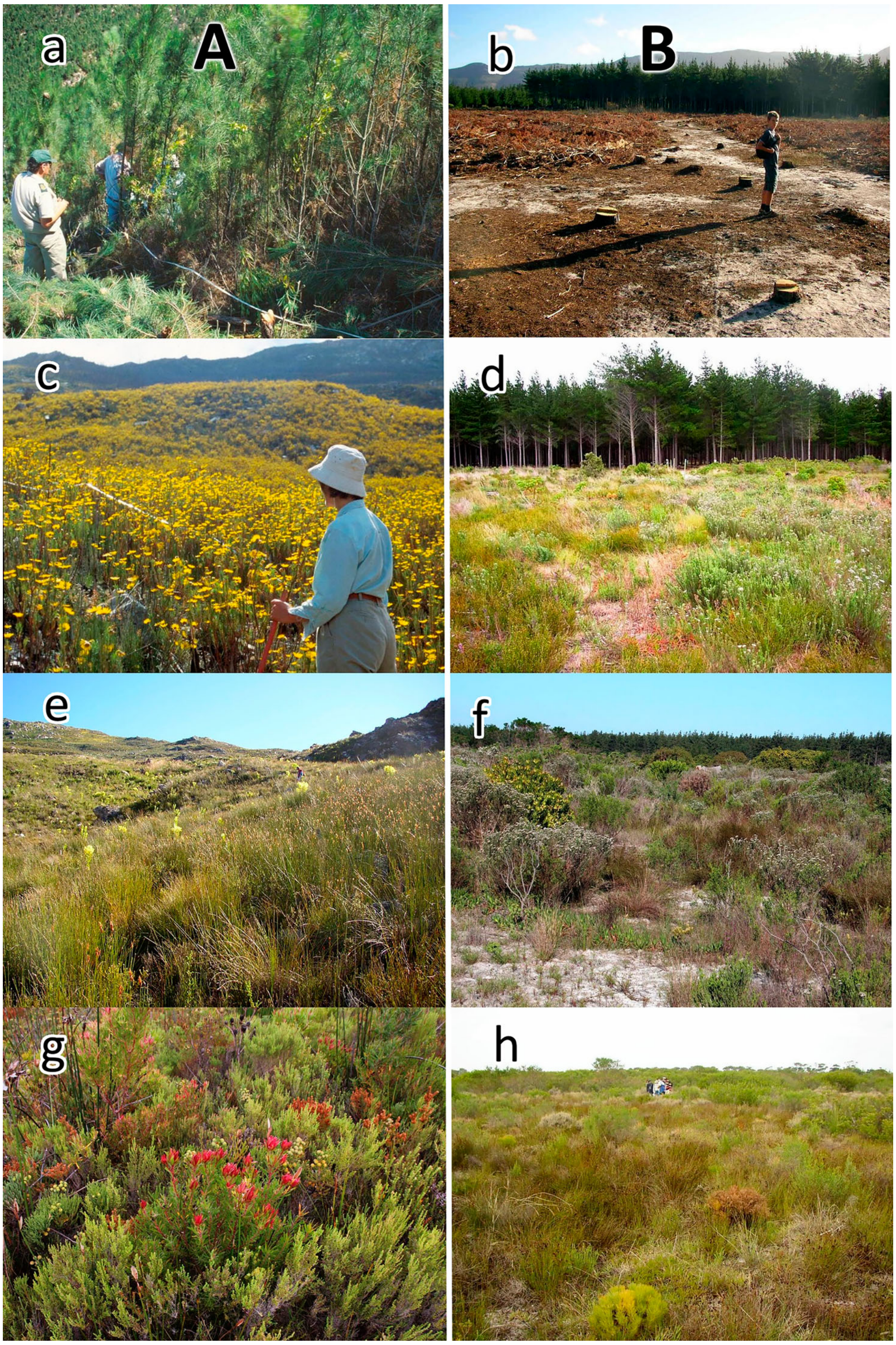

Figure 3. A, B. Case studies of ecological restoration stages following dense alien invasion in the Core Cape Subregion. A. (Left panel) *Pinus pinaste*r and *Hakea sericea* in mountain fynbos; (a) young alien trees felled and one year later slash burnt in a wild fire; (c) the low biomass fire resulted in good spontaneous succession (3 years), but overstorey proteoids were sparse (e, 6 years), (Holmes & Marais, 2000), (g) reference vegetation. B. (Right panel) *Pinus radiata* in lowland fynbos; large timber was harvested and remaining slash burnt in autumn, (b) good spontaneous succession from the soil seed bank (d, 3 years), overstorey proteoids were locally extirpated, requiring re-introduction, and resprouter shrubs were few (f, 6 years) Petersen *et al*., 2007), (h) reference vegetation. Photo credits P.M. Holmes (a, c, e), A.G. Rebelo (b, d, f, g, h).

invasions quite often do not cover the entire landscape. Coupled with the higher persistence of soil-stored seed banks in these ecosystems, this means that active restoration may not always be warranted (Figure 3 A). Exceptions are for older dense alien stands or exited plantations that are extensive such that seed banks are depleted (Galloway *et al*., 2017) and seed dispersal opportunities from adjacent stands are insufficient to initiate recovery. Initial control in these extensively invaded areas should be implemented before alien tree biomass becomes too high, followed by post-fire active restoration interventions. It is preferable to re-introduce fynbos species by locally sourced seed to restore genetically

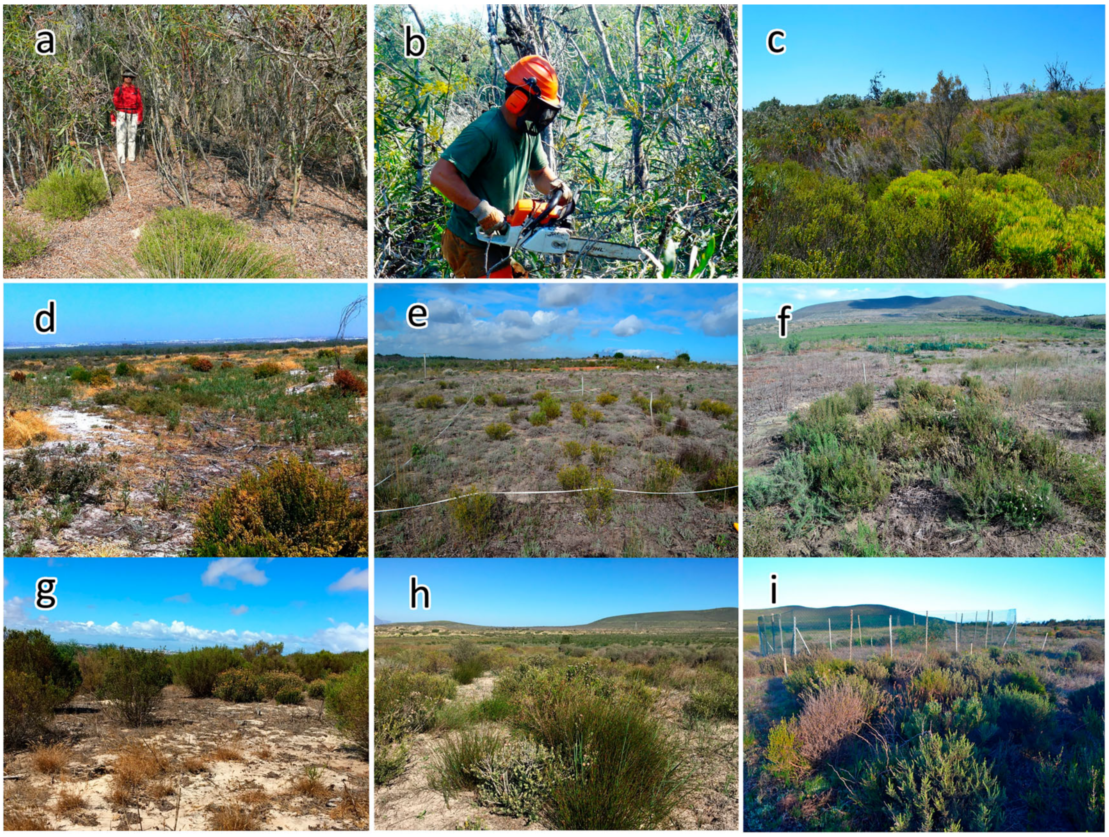

Figure 3. C. Case study of ecological restoration following dense *Acacia saligna* invasion in lowland fynbos; (a) dense *Acacia saligna* showing canopy die-back by gall-forming fungal biocontrol agent, (b) clearing operations in progress, (c) reference site, (d, 3 years and g, 6 years) after Fell & Stack initial clearing method: limited recruitment by fynbos or acacias, bare ground invaded by herbaceous weeds; (e, 3 years and h, 6 years) after Fell & Burn initial clearing method: mass acacias recruitment cleared, sparse fynbos recruitment but higher diversity than (d,g); (f, 3 years and i, 6 years) after Fell & Burn plus fynbos sowing, post-fire sowing greatly improved fynbos growth form structure, diversity and cover (Hall, 2018). Photo credits: P.M. Holmes (a, b, d, g, h), S. Hall (c, e, f, i).

diverse and locally adapted populations. Serotinous Proteaceae are the easiest component to re-introduce by scattering seeds onto bare ground in autumn, as this closely mimics their post-fire recruitment strategy. For other reseeder species, it is advisable to pre-treat the seeds with smoke (Brown, 1993) and/or heat as appropriate (Hall *et al.*, 2017). Some key structural elements are difficult to restore by seed, such as fynbos resprouter shrubs (Hall, 2018), and it may be necessary to re-introduce these by more expensive nursery rootstock (plugs or plants).

Lowland fynbos

The same principles above apply to lowland fynbos ecosystems, except that there is greater accessibility to harvest wood products and thus better integrate removal with control operations. However, various factors in the lowlands act synergistically to result in active restoration being required in most cases of dense alien invasion. These are that: (1) acacias with their higher ecosystem-level impacts are the predominant invader; (2) key fynbos structural components have lower seed persistence than in mountain fynbos, conferring lower restoration potential; and (3) the landscape context is usually one of fragmentation by transformed land (agriculture or urban developments), reducing long-term fynbos recolonisation potential. Legacy effects of nutrient-rich soils, large acacia seed banks and secondary alien invasions also imply that pro-active interventions are necessary to initiate recovery along a restoration trajectory. Fortunately, elevated NO_{-3} in the soil did not reduce germination or establishment of a widespread lowland proteoid, indicating good potential for active restoration provided that secondary invasions are controlled (Nsikani *et al.*, 2018b). Granivory and soil disturbance by fossorial mammals is a further barrier to active restoration in lowland fynbos and it is advisable to erect raptor perches and owl boxes to hasten the reduction of granivore population sizes and to consider delaying fynbos sowing by a year until granivore populations have naturally declined. Such impacts are less severe under dense pine, which better preserves the fynbos soil-stored seed bank and confers higher restoration potential than does acacia (Figure 3 B; Mostert *et al.*, 2017). To meet an ecological restoration goal, sufficient long-term management commitment and resources will be required. Thus the appropriate restorative goal for invaded lowland fynbos must be considered carefully, and will depend on the long-term vision for the land in question and the support of potentially diverse groups of stakeholders.

Riparian vegetation in the Cape Floristic Region

Headwater and foothill streams

Studies of soil-stored seed banks indicate that a functional cover of herbaceous and low shrub growth forms may emerge spontaneously after dense alien clearance and fire,

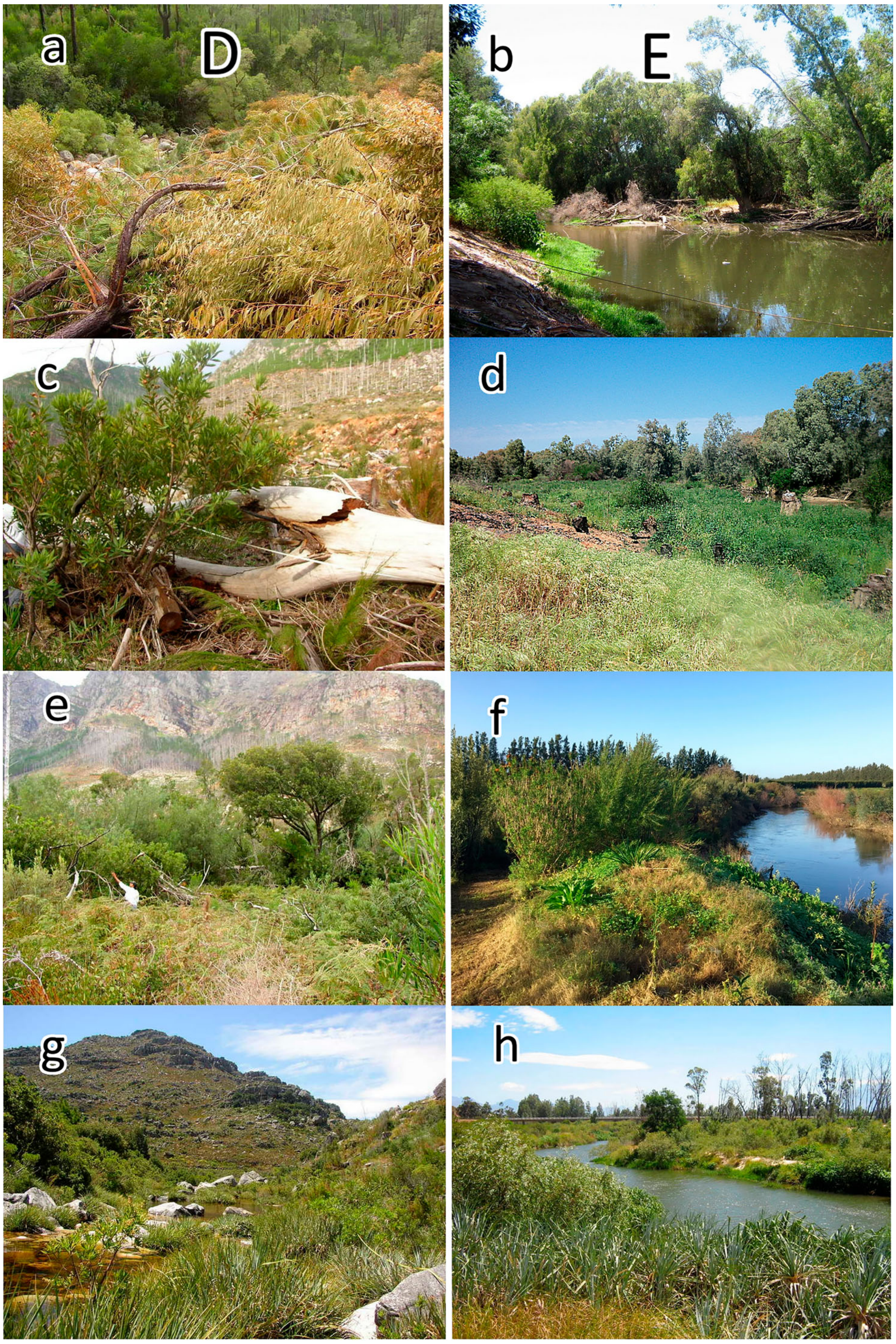

Figure 3. D,E. Case studies of ecological restoration stages following dense alien invasion in riparian zones. D. (Left panel) *Acacia mearnsii* and *A. longifolia* in headwater streams; (a) acacias felled; spontaneous succession is optimised following a Fell & Remove initial clearing method, (c, 3 years) persisting riparian shrubs resprout, other species colonise from seed bank, (e, 6 years) good recovery of growth form structure, (g) reference vegetation, (Blanchard & Holmes, 2008). E. (Right panel) *Eucalyptus camaldulensis* in lowland rivers shades out most other riparian vegetation (b), surrounding landscape is usually modified by agriculture, (d, 3 years) after clearing, a few native plants recolonise but herbaceous weeds dominate, (f, 6 years) active restoration is needed and planting of riparian scrub rootstock is quite successful if irrigated initially (Ruwanza *et al.*, 2013b), (h) reference sites are scarce, here wetbank species persist. Photo credits: P.M. Holmes (a–g), A.J. Rebelo (h).

although acacia seeds will also germinate and require intensive follow-up control (Fourie, 2008; Vosse *et al.*, 2008). Where the initial alien control method is Fell & Remove, 95% of invaded sites spontaneously recovered a growth form structure indistinguishable from reference sites (Figure 3 D; Blanchard & Holmes, 2008). However, if other methods are applied, such as Fell Only, or Fell & Burn, recovery may be protracted, or arrested by secondary grass invasions, respectively, and active restoration is recommended (Blanchard & Holmes, 2008; Reinecke *et al.*, 2008; Fill *et al.*, 2017). Active restoration by

Table 2. Passive restoration. Descriptions of the most commonly applied methods used for invasive alien tree control

Control method*	Description	Targeted alien species; habitat	Positive restoration impacts	Negative restoration impacts
Initial control				
Fell Only	Trees felled and stump-treated with herbicide if species coppices	All species; mostly used in mountain fynbos	Alien fuel rots *in situ*, while native species co-existing in the vegetation recover and replenish native seed banks	Dense alien fuel may smother regrowth of native vegetation; a wild fire may damage soil and native seed banks
Fell & Stack	Trees felled and stump-treated with herbicide if species coppices; fuel placed into tight stacks	All species; mostly used in lowland fynbos	High fuel loads concentrated in stacks reducing risk of damage from summer wild fire; bare ground created for potential fynbos recruitment	Without fire, spontaneous succession by soil-stored fynbos species may be slow; burning of stacks – even in winter – could cause local damage to soil and seed banks and stimulate acacia seed bank to germinate near stacks
Fell & Burn	Trees felled and stump-treated with herbicide if species coppices; fuel burnt in prescribed burn	Mostly applied following pine harvesting, but sometimes in other situations if a wild fire occurs post-felling; mainly in mountain fynbos	Removes alien fuel and litter; volatilises some of the accumulated nutrients; stimulates fynbos soil-stored seed banks to germinate	If alien stand >10 years, high fuel loads may damage soils and fynbos seed banks if burnt in summer; winter burn may be suboptimal for fynbos establishment; fire stimulates acacia seed banks to germinate and re-invade cleared area
Burn Standing	Untreated trees burnt in a prescribed fire: foliage needs to be sufficiently dry and weather suitably warm and dry for trees to be killed; may be difficult to obtain permit	Mostly applied to non-coppicing species, such as pines and hakeas; mainly in mountain fynbos	Lowers fuel loads at soil surface and risk of wild fire damaging soils and fynbos seed banks; stimulates fynbos soil-stored seed banks to germinate	Standing dead fuel may reduce efficacy of follow-up control; could spread seed of alien serotinous species (pines, hakeas)
Fell & Remove	Trees felled and stump-treated with herbicide if species coppices; larger wood removed from site	Pine, acacia and eucalypt where wood is economically viable to extract and where felled, large trees could damage ecosystem; mostly in riparian and coastal habitat	Lowers fuel loads and risk of wild fire damaging soils and fynbos seed banks; provides space for spontaneous succession; best method in riparian ecosystems	Without fire, spontaneous succession of soil-stored fynbos species may be slow
Kill Standing	Trees ringbarked or frilled to kill roots and ultimately whole plant	Mostly applied to suckering species such as poplar and black wood, but also useful for large trees such as eucalypts and black wattle where wood cannot be harvested; mostly in riparian habitat	Retains large fuel above ground so that a fire causes less damage to soil and fynbos seed banks; in riparian areas lowers soil disturbance and potential erosion risk	Standing dead fuel may reduce efficacy of follow-up control; in riparian areas stems will eventually fall into river and could cause log-jams downstream
Aerial spraying	Trees sprayed from above with herbicide (by helicopter or boom-sprayer)	All species; used for dense, extensive stands or where access for manual methods may be difficult; mountain or lowland fynbos	In dense stands, kills trees standing so that a fire would cause less damage to soil and fynbos seed banks	Has a negative impact on fynbos community structure and species richness
Biological control	Successful biological control agents reduce growth and/ or reproductive output of alien species	Hakeas and acacias; all ecosystems	In cases where the growth and life-span of trees is reduced, retains spontaneous succession as a viable strategy longer	Usually not effective alone and needs to be combined with another control method
Follow-up control				
Hand pull	Seedlings and saplings uprooted by hand	Seedlings of all species; not useful for coppice; all ecosystems	If done carefully has little negative impact on spontaneous succession	In dense alien patches could cause soil disturbance and negatively impact on fynbos seedlings

(*Continued*)

Table 2. Continued.

Control method*	Description	Targeted alien species; habitat	Positive restoration impacts	Negative restoration impacts
Fell only	Saplings are cut low and stump-treated with herbicide if species can coppice	Saplings of all species; not useful on coppice; all ecosystems	If herbicide is carefully applied to stumps has relatively little impact on spontaneous succession	Herbicide drift has been noted for treated coppicing species, negatively impacting spontaneous succession
Cut below root crown	Saplings are cut below root crown, generally below soil level	Saplings of coppicing species, such as *Acacia saligna;* lowland ecosystems	Has lowest negative impact on spontaneous succession	Time-consuming and the most expensive method; only suitable for low density alien recruitment
Foliar spray	Dense patches of seedlings or saplings are sprayed with herbicide	Mostly used for acacia species; mainly in lowland and riparian habitats	Cost-effective where fynbos recruitment is anticipated to be negligible	Herbicide drift kills adjacent fynbos dicotyledons, negatively impacting on spontaneous succession
Biological control	Successful biological control agents reduce growth and establishment of alien species	Growth rate and longevity of *Acacia saligna* is reduced by biological control agents; seed production is reduced in several species	Biological control agents that reduce growth of trees may promote co-existence of fynbos and alien seedlings and delay timing or reduce intensity of follow-up control required	Usually not effective alone and needs to be combined with another control method

*The Working for Water website provides information on commonly applied control methods: https://www.environment.gov.za/sites/default/files/docs/controltables.pdf; see also 'Aliens and their management' in *Fynbos Ecology and Management* (Esler et al., 2014).

Table 3. Items to include when objectively assessing the additional costs of active restoration. Actual costs will vary with each project, and depend on availability of viable propagules and distance to sources. The size and relative accessibility of sites will also affect costs.

Item	Description of components for costing
Seed collecting	Plan and organise field trips to collect seeds of target species: generally seed mixes will require several commoner species to be collected for each main structural component of the ecosystem. Costs include professional expertise, labour, seed collecting equipment and travel.
Seed processing	Treat seeds against fungal decay and predation and store under suitable conditions until required. Pre-treat seeds if required ahead of sowing (e.g. smoke and heat pre-treatment) and prepare seed mixes for sowing. Costs include professional expertise, labour, storage facilities and seed processing equipment and materials.
Sowing	Plan and organise field trip to prepare ground (e.g. raking of litter to expose bare soil if required) and sow ensuring correct timing. Costs include professional expertise, labour and travel.
Propagation	Propagation may be required for key structural groups that do not germinate well or readily establish from seed (e.g. some obligate resprouter shrubs). Cutting material will need to be collected at the correct season and nursery stock prepared in plugs or bags. Costs include professional expertise, nursery facilities and equipment, labour and travel.
Planting	Plan and organise field trip to plant out rooted material in the correct season (i.e. once soil is sufficiently moist). Costs include professional expertise, labour and travel.
Monitoring	Monitor the relative success of species re-introductions to indicate whether follow-up re-introductions are necessary. Costs include professional expertise and travel.

sowing a riparian scrub seed mix increased both diversity and abundance of native plant species, but acacia follow-up control is essential to sustain the benefits of this intervention (Pretorius *et al.*, 2008). A further benefit of actively restoring riparian scrub in highly degraded streams is that aquatic invertebrate species diversity and endemic taxa respond positively to the re-establishment of native species following alien tree clearing (Samways *et al.*, 2011; Gerlach *et al.*, 2013).

Lowland rivers

Lowland rivers are more likely to have landscape-scale barriers to restoration such that restoring to a historic riparian community is an unfeasible goal. In most cases lowland river reaches are below impoundments that alter hydrological and geomorphological functioning and are embedded in a fragmented landscape of agricultural or urban developments. Thus the key disturbance regimes of flooding (annual as well as episodic, large floods) and fire seldom operate to structure these riparian ecosystems and associated wetlands. Such landscape-level changes may have been operating for many decades, incurring a response in natural remnants of change towards communities more typical of riparian fire refugia, with a higher representation of thicket resprouter and Afrotemperate Forest tree species.

Studies in eucalypt-invaded lowland riparian zones indicate some modest potential for spontaneous succession from soil-stored seed banks, although large seed banks of herbaceous

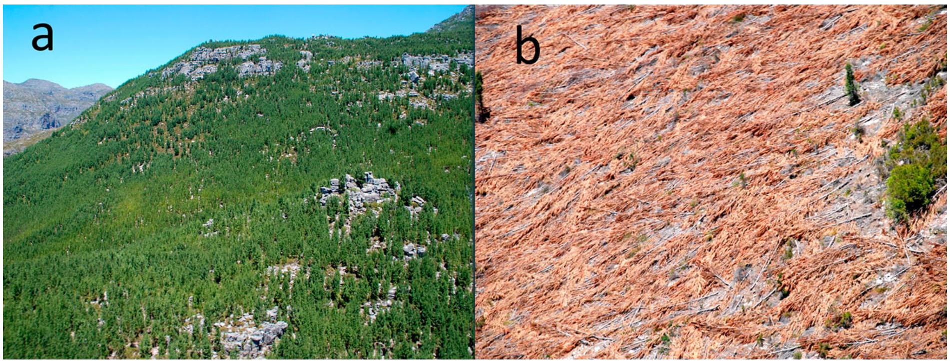

Figure 4. Dense invasions of alien pine trees (*Pinus pinaster*) in the upper catchment of the Berg and Riviersonderend Rivers in the Western Cape (a) and an adjacent area where these trees have been felled in 2019 control operations (b). Sites such as these will require active restoration, which needs to be explicitly factored into control plans before a decision is made to initiate control operations. Photo credits: B.W. van Wilgen.

weeds may thwart this potential (Tererai *et al.*, 2015b). Active restoration is recommended to avoid protracted recolonisation by native species; however, it was found that after alien clearance, sowing of viable seeds was not very successful (Ruwanza *et al.*, 2013a) and other methods of plant establishment, including nursery rootstock (plugs or plants) and/or irrigation may be needed to re-establish riparian shrubs and trees in this ecosystem (Figure 3 E). For lowland rivers in modified catchments, vertebrate-dispersed shrub and tree species are an important structural element to be targeted in active restoration. A stepwise, four-stage thinning method can be applied to promote establishment of this guild (Ruwanza *et al.*, 2013c), through reducing competition for the existing native plants, retaining bird-perches for seed dispersal and to provide space for seed or seedling re-introduction. In lowland rivers, rehabilitation of an ecosystem function, such as soil erosion control, may be a more appropriate goal than restoration of a historic plant community, depending on the particular context of the alien-invaded site.

PRINCIPLES AND IMPLICATIONS FOR MANAGEMENT

Principles for optimising spontaneous succession

We have discussed the complexities of ecological restoration following alien plant invasion, and put forward the elements of best practice that, if diligently implemented, would provide the best chance of achieving the restoration of ecosystem structure and function. However, the problem of alien plant invasions in the CCS is extensive; invasions cover an estimated 265 000 ha (with a cover of 6% or more) in provincial nature reserves and national parks alone (van Wilgen *et al.*, 2016b). Much of this is in rugged and inaccessible mountain catchment areas. By 2015, national and provincial government conservation agencies had spent at least R568 million (net present value in 2015) on alien plant control operations in the CCS, and substantial amounts continue to be spent each year (van Wilgen *et al.*, 2016b). Recently, these efforts have been supplemented by NGOs like WWF (South Africa) and The Nature Conservancy (Stafford *et al.*, 2018) as well as by the private sector (van Rensburg *et al.*, 2017). Despite this, funds are insufficient to address alien tree invasions across the entire CCS, and if the funds are spread too thinly the goal of ecological restoration will not be met. In addition, active restoration is not factored into most current control operations, although warranted in many cases (Figure 4). Active restoration is an additional, expensive undertaking that requires long-term commitments. Unfortunately, there are almost no data on the costs involved in successful restoration, although Hall (2018) estimated costs of seed collecting, processing and sowing seeds to be approximately R10500/ha (2020 Rand value). Given that alien plant control projects are at high risk of failure if adequate provision for restoration is not made, and because such provisions are very costly, we strongly recommend that no alien plant control project should be initiated without first establishing what it would take to restore the site to a desired state, and whether this is affordable. This underscores the importance of prioritisation and triage in restoration planning, at both local and regional scales.

The first principle is to act early in the invasion process before biotic or abiotic thresholds are crossed; once these are breached, active restoration intervention becomes necessary to repair the ecosystem. This means that low-density invasions and sites with recent, dense invasion should be prioritised to optimise the benefits of spontaneous succession and achieve the greatest long-term ecological gains from alien control. However, conflicts in decision making may arise where immediate economic and social benefits compete with optimising biodiversity benefits and long-term ecological sustainability. Cost-benefit analyses, combined with system dynamics and interactive tools such as analytical hierarchical process (Crookes *et al.*, 2013; Mostert *et al.*, 2018), can assist in articulating appropriate ecological restoration goals and prioritising sites in each region in order to achieve improved long-term ecological functioning (Currie *et al.*, 2009; Anderson *et al.*, 2017). Some strategic water source areas (Nel *et al.*, 2017) and critical biodiversity conservation areas (Skowno *et al.*, 2019) may be exceptions where dense and long-invaded areas could be prioritised for clearing, although they have lower potential for spontaneous succession and higher restoration costs. However, these areas should only be cleared where sufficient resources are available for active restoration interventions. In lower priority areas with low restoration potential the primary objective should be to contain the invasion and prevent further spread.

The second principle is that follow-up alien control is essential to maintain the gains of initial interventions, both in areas recovering spontaneously and in areas where active restoration has been implemented. Benefits from initial investments can be quickly lost if follow-up control is not planned and implemented optimally (van Wilgen *et al.*, 2016b). This requires long-term management commitment at a site, including extending over two or more fire-cycles as fire provides a window for recolonisation by both native and alien species.

Thirdly, applying appropriate initial control methods effectively is crucial for minimising the extent of subsequent follow-up control required and costs (Cheney *et al.*, 2019). Poorly executed initial clearing work can negatively impact on native species, for example through the resultant need to apply herbicide, and lead to poor native recovery and a requirement for active restoration.

Fourthly, integrated control is a crucial element in long-term management strategies for most invasive alien trees and shrubs in the CCS, including appropriate biological, mechanical or chemical control methods (Moran & Hoffmann, 2012) and fire management. Including biological control can potentially slow the rate of invasion and the intensity of invasion impacts, by reducing the growth rate, life-span or seed production output of an alien species. This may extend the effectiveness of spontaneous succession in invaded vegetation for a longer period, potentially until resources are available to initiate control.

A fifth principle for fire-adapted ecosystems is that wildfires and prescribed burns should be included in all planning scenarios. Judicious use of prescribed dry-season burns to remove alien slash and stimulate fynbos germination from seed banks may accelerate spontaneous succession following clearance of alien trees. Because most invasive alien trees in the CCS are fire-adapted, a prescribed burn should only be used where spontaneous succession is anticipated or where fynbos seed mixes are to be sown. In addition, prescribed burns should only be used where alien propagules can be controlled, either by being killed in the fire (e.g. seeds or seedlings of felled pines and hakeas) or where soil-stored seed banks are small enough for alien seedlings to be efficiently removed. In the case of dense acacia with large soil-stored seed banks, fire may not be a useful restoration tool and it may be prudent to delay slash burning until granivores have been given sufficient time to reduce the alien seed bank to a manageable density.

Finally, a sixth principle is to recognise the need for flexibility and adaptive management. This implies that targets need to be set for gauging success as the vegetation recovers; should the targets not be met, then operational plans need to be adapted to cater for unforeseen outcomes. In addition, management teams must be able to adjust their work programmes to cater for unforeseen disruptive events, most notably unplanned wildfires that frequently disrupt control operations (van Rensburg *et al.*, 2017). This flexibility is largely absent under the current operating rules required by major funders (van Wilgen & Wilson, 2018) and creative ways may need to be found to address such contingencies.

Hidden costs of spontaneous succession

The aforegoing discussion assumes that passive restoration should be the favoured approach for managing invaded landscapes, because it avoids the substantial additional costs implicit in implementing active restoration. However, where the goal is to restore ecosystem structure and function, there may be instances where a structural component remains absent following spontaneous succession, for example the fynbos overstorey proteoid shrub layer. In this case it is relatively inexpensive to remedy the deficiency by collecting seed-bearing cones of proteoids from adjacent vegetation remnants and sowing seeds onto bare ground in autumn prior to the winter rainfall season. If suitable active restoration goals are put in place from the start, it is possible that at a low additional cost to the passive restoration budget, structure and function of the restored vegetation can be greatly improved. Currently this practice is not explicitly factored into management planning, and we strongly advise that it should be included (Figure 4). This in turn may suppress further recruitment of invasive plants and reduce the future costs of alien follow-up control (Pretorius *et al.*, 2008).

There are other unanticipated costs to passive restoration (Zahawi *et al.*, 2014), often relating to the longer time required for this approach to succeed. Slow recovery following spontaneous succession can be perceived as project failure and this could lead to disillusionment, disinvestment and site abandonment. A task for research is to develop practical indicators that can be applied at different stages to assess and demonstrate whether succession is proceeding as anticipated. Natural areas cleared of alien trees and left to passively restore can be viewed as unused or degraded land by some stakeholders; this perception could be a high risk in developing countries like South Africa, where there is a shortage of land for housing and farming. Herbivory by domestic livestock or inappropriate stocking with wild ungulates is often a major challenge in the early stages of passive restoration and expensive fencing may need to be erected and maintained, requiring ongoing travel and labour expenses to check that grazing disturbance and other intrusions are kept out of the area.

Management challenges: issues and constraints

Alien plant invasions present many diverse challenges to natural resource managers, but good strategic planning (e.g. five-year strategic plans that articulate long-term goals) and annual plans of operation (including budget) can greatly improve implementation and outcomes, provided that some flexibility is included to allow for unanticipated challenges and issues (Figure 5). In the fire-prone fynbos, wild fires are an ever-present possibility during the hot, dry season that could disrupt planned alien control and restoration initiatives. In some cases such fires offer opportunities to circumvent the initial alien control treatment, provided that resources can be rapidly re-deployed for post-fire follow-up control (not the case in current government-funded control initiatives), thereby promoting spontaneous succession. In other cases, fires are disruptive, for example where felled alien slash can burn at high intensity, resulting in damage to the soil (Richardson and van Wilgen, 1986). In such cases, mechanical measures to prevent or mitigate erosion may be required, sometimes in combination with revegetating the vulnerable areas.

There is a tension between optimising alien control and optimising ecological restoration that managers must address. Most funding for alien control is currently supplied by the national resource management programmes, such as Working for Water (WfW). The original goal of WfW was to control alien trees to protect water resources, while simultaneously utilising the opportunity to create employment (van Wilgen *et al.*, 1998). However, sourcing funding from the Expanded Public Works Programmes means that employment creation has often become the primary goal. As discussed above, the restoration of self-sustaining and functional ecosystems can only be achieved in situations where alien clearance would result in spontaneous

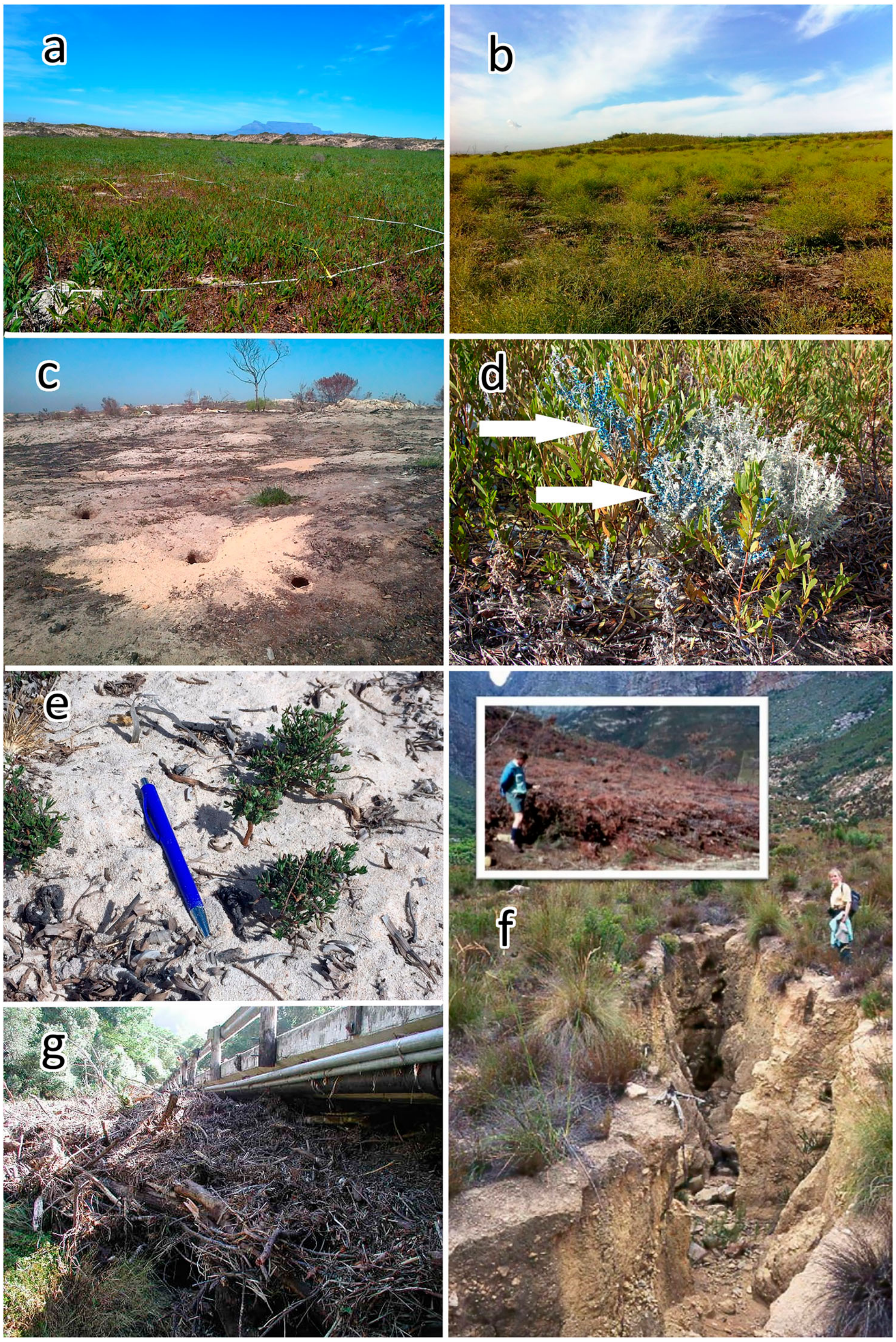

Figure 5. Examples of ecological restoration challenges following dense invasion by alien trees in the Core Cape Subregion. (a) Mass germination of alien *Acacia saligna* from soil-stored seeds after an initial Fell & Burn clearing method resulted in expensive follow-up control. (b) Secondary invasion by alien *Raphanus raphanistrum* following control of acacias in lowland fynbos, notably in bare ground areas after the Fell & Stack initial clearing method. Secondary invasions by weedy herbaceous species may be promoted by soil nutrient enrichment under acacias. (c) Disruption by fossorial mammals, including soil disturbance from mounding, granivory and herbivory. Here, gerbil (*Tatera afra*) activity is evident after acacia clearance in lowland fynbos; high acacia seed production maintains populations of granivores. (d) Foliar spraying of herbicide to kill alien regrowth after poor initial clearing operations or fire may drift onto native species thus disrupting spontaneous succession, as seen by blue dye on native *Metalasia* species. (e) Grazing by antelopes or domestic livestock can impede re-establishment of perennials following alien control; here heavy browsing of ericoid shrubs occurred and antelope numbers should be kept below carrying capacity until vegetation is restored, or the restoration areas fenced off. (f) Unplanned fire through dense alien slash may cause a high-intensity burn with most heat generated on or near the soil surface, resulting in soil damage, loss of native propagules, death of lignotubers or other resprouting structures, and subsequent extensive soil erosion during the rainy season. These impacts may be lessened by removing large fuel and/or burning slash under cooler conditions while soil remains moist. The inset shows dense slash of felled *Hakea sericea* shrubs at Wemmershoek; the main image shows the same area 16 years later. Severe erosion was caused after an intense slash fire that induced soil water repellency. This had a major impact on the trajectory of succession. (g) In riparian zones, felled alien slash may be washed downstream during floods, causing log-jams against infrastructure that can cause major damage and incur high repair costs. The Fell & Remove initial clearing method is recommended to avert such damage; here *Acacia mearnsii* slash brought downstream in a large flood resulted in bridge collapse. Photo credits: P.M. Holmes (a–e); D.M. Richardson (f, g).

succession (typically where native soil seed banks persist) and where the appropriate clearing methods are applied that do the least damage to native vegetation and are implemented efficiently. In reality, clearing is not always implemented efficiently (McConnachie *et al.*, 2012; Kraaij *et al.*, 2017; Cheney *et al.*, 2019), resulting in downstream funding shortfalls to deal with alien regrowth. Often herbicides are over-utilised to control alien regrowth to the detriment of native vegetation recovery (P. M. Holmes, personal observations). The WfW Norms Table sets out the person day/hectare standard for the different alien species, methods, densities and terrain (Neethling & Shuttleworth, 2013); all agencies and contractors must adhere to these norms, leaving little flexibility to implement alternative methods or active restoration interventions. Furthermore, procurement constraints within this centralised government system do not permit the rapid release of resources to deal with unplanned events, such as fires. The few exceptions where active restoration may be funded by WfW are for riparian zones where there is a risk of soil loss during floods, and terrestrial steep slopes with severe soil damage from intense fires (C. Marais, personal communication 2020).

The disadvantage of the public-works model discussed above is that the agencies tasked with natural resource management rely almost entirely on this funding stream and cannot build their own capacity and expertise to manage invasions optimally (van Wilgen *et al.*, 2016b). Managers wishing to actively restore invaded areas are limited by the constraints imposed by the funder and additional private funding sources would need to be sought. An avenue worth exploring is to create partnerships between the funder currently focussing on alien control and volunteer-based NGOs seeking involvement in ecological restoration, whereby the latter may implement the active restoration components of projects. The efficiency of initial clearing operations should be improved through increased training, supervision and monitoring to prevent the further spread of invasive aliens and to optimise restoration through spontaneous succession. Long-term, sustainable progress will only be achieved if sufficient priority is given to the goal of achieving ecological restoration and the public works model is modified to retain skilled staff on a more permanent basis to improve efficiency.

We have conceptualised the main findings of ecological restoration following alien invasions as a schematic of restoration costs versus duration of dense invasion (Figure 6), which may be used in combination with individual invader species decision trees (Figure 2 a–c) to assist in planning realistic management interventions at both regional and local scales. In the majority of mountain catchment cases, including headwater riparian ecosystems, restoration of ecosystem structure and functioning can be achieved by prioritising and carefully clearing sites where spontaneous succession is anticipated, and in more degraded sites by implementing relatively low-cost active interventions such as sowing local overstorey proteoids or riparian pioneer shrub species after alien clearing and fire. Where resources are limited, triage should be applied and the most long-invaded, dense stands contained and only cleared once resources are available for active restoration interventions. For example, McConnachie *et al.* (2016) concluded that control of alien pines in the Hawequas mountain complex might have prevented a larger area from becoming invaded if it had focussed all of its effort on untransformed, less densely invaded land and not on abandoned closed-canopy plantations. In lowland fynbos, where spontaneous succession is less likely after dense invasion, many ecosystems are highly threatened and natural remnants from which to source seeds for active restoration are scarce, therefore any areas with some modest potential for recovery should be prioritised for alien clearing as a matter of urgency. In dense alien stands, lowland fynbos restoration requires the

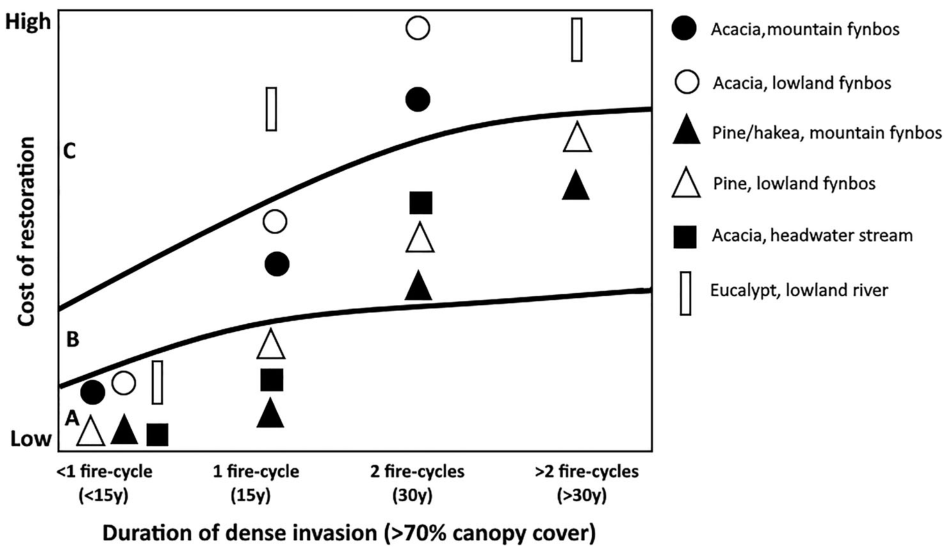

Figure 6. Relative costs (including labour) to restore native ecosystem structure and function for different durations of dense (>70% canopy cover) alien stands of dominant invader species in four major ecosystem types in the Core Cape Subregion. Lines represent thresholds, beyond which different actions apply, A = spontaneous succession, B = small active restoration intervention (e.g. sow overstorey proteoid seed), C = active restoration required. Less dense invasions spontaneously recover, provided that appropriate alien clearance methods are applied and implemented effectively. More extensive areas of dense invader stands generally have lower restoration potential and those of long-duration invasion should be contained and only cleared sequentially as resources become available for simultaneous active restoration interventions.

sourcing and re-introduction of all major structural guilds after clearing which is expensive and may only be warranted in protected areas where biodiversity conservation is the primary goal. In most lowland riparian areas ecological drivers have been modified by upstream impoundments, water abstraction and surrounding land-use such that an ecological restoration goal may not be appropriate and a lesser goal, such as rehabilitation to prevent soil erosion after alien clearing, using native species in support of local fauna, would be a more realistic management option.

CONCLUSIONS AND FUTURE DIRECTIONS

This review has addressed the question of whether spontaneous succession is a viable strategy to restore alien-invaded ecosystems in the CCS. We conclude that:

1. Spontaneous succession can be relied upon in areas with low to medium-density invasions and for dense invasions where a diversity of growth forms persist in above-ground vegetation and/or in soil-stored seed banks.
2. Site-scale factors that mediate the potential for spontaneous succession include: the density of the invasive stand, the duration of dense invasion, the identity of the invader, the ecosystem type and method/efficiency of control. Landscape-scale factors also influence the viability of spontaneous succession; there is greater potential in sites embedded within natural vegetation compared to sites in a fragmented, transformed environment where large-scale ecological and hydrological processes are modified.
3. Sites with low spontaneous succession potential will require active restoration interventions to overcome biotic and/or abiotic barriers to recovery and to prevent immediate re-invasion by the targeted alien species or secondary invaders.

The recent international call to massively scale-up ecological restoration globally means that we urgently need to consider how to better integrate restoration and alien control processes and initiatives. To achieve this in the CCS will require the following:

1. Improved strategic planning and prioritisation protocols: because resources are limited and funding models constrained, less degraded sites with greater potential for spontaneous succession should be prioritised for alien clearing, with a view to halting further invasions and optimising ecological restoration. Exceptions may be in sites of high ecosystem service or biodiversity conservation importance which have low spontaneous succession potential; here resources must be deployed in active restoration.
2. Improved operational planning and implementation procedures: at the local (site) scale, it is important to plan according to the same principles as in (1). In addition, managers need to improve the training of workers and the monitoring of control methods and outcomes to reduce the negative impacts of poor implementation on spontaneous succession outcomes.
3. More flexibility in both longer-term strategic plans and annual plans of operation is required to allow for adaptive management to deal efficiently with unforeseen challenges, such as unplanned fires.

ACKNOWLEDGEMENTS

We acknowledge support from the DSI-NRF Centre of Excellence for Invasion Biology over the past 15 years. DMR thanks the Oppenheimer Memorial Trust (grant 18576/03) and the National Research Foundation (grant 85417); KJE the Water Research Commission (C2019/2020-00034) and KJE & PMH the Hans Hoheisen Charitable Trust for additional support. Views expressed in this paper have been shaped by interactions with many collaborators over almost three decades of research on restoration in the Core Cape Subregion.

DISCLOSURE STATEMENT

No potential conflict of interest was reported by the authors.

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